

Morphology of *Scapter* (Hymenoptera: Anthophila: Colletidae), with description of three new species and taxonomic status of five Cockerell taxa

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ABSTRACT

The morphology of the bee genus *Scapter* Lepeletier de Saint-Fargeau & Audinet-Serville, 1828 (Hymenoptera: Anthophila: Colletidae) is investigated. Additionally, three new species are described and the taxonomic status of five, previously overlooked Cockerell taxa is evaluated.

Scapter shows hitherto under-appreciated diversity in the following morphological features: galeal comb, postmentum, lacinia, labrum, facial fovea, pronotum, anterior probasitarsal brush, pretarsus and metabasitibial plate. The monophyly of *Scapter* is not supported by unambiguous apomorphies, but is defensible by the congruence of various qualitative characters (e.g. premental fovea, hindleg and sternal scopa in female, T2 fovea, two submarginal cells).

The new species are: *Scapter pruinosus* Davies, sp. n. (both sexes), *S. pyretus* Davies, sp. n. (both sexes) and *S. viciniger* Davies, sp. n. (male only). The taxonomic status of five species described by Cockerell in 1944, and subsequently overlooked, is addressed. They are all found to be synonyms of other *Scapter* species, except one, which is found to be a *Ctenoplectrina* species (Apidae: Apinae: Ctenoplectrini). The new synonymies are: *S. subincertus* Cockerell (= *S. niger* Lepeletier de Saint-Fargeau & Audinet-Serville), *S. brunneipennis* Cockerell (= *S. niger*); *S. merescens* Cockerell (= *S. leonis* Cockerell); *S. sinophilus* Cockerell (= *S. algoensis* (Friese)). *Scapter ugandica* Cockerell becomes *Ctenoplectrina ugandica* (Cockerell) as a new combination.

KEY WORDS: Afrotropical, Colletidae, *Scapter*, morphology, taxonomy, new species, bees.

INTRODUCTION

Scapter Lepeletier de Saint-Fargeau & Audinet-Serville, 1828 comprises small to medium-sized (3.5–14 mm long), non-metallic, ground-nesting, solitary bees (e.g. Fig. 1), restricted largely to southern Africa (but with an outlier record from Kenya). The genus is relatively large (44 valid species prior to this publication), and much morphological diversity is encompassed by the genus (e.g. Fig. 2). By possession of their short, weakly bilobed glossa (bearing a glossal brush and pre-apical fringe), *Scapter* clearly belongs in the Colletidae (Michener 1944: 237, 2000: 161–163; Engel 2005: 13–14, 30). Within the colletid clade, *Scapter* has traditionally been accommodated in the Colletinae (e.g. Michener 2000), a paraphylum that has recently been sub-divided into smaller apparently monophyletic entities (Engel 2005; Melo & Gonçalves 2005; see also Ascher & Engel 2006). We have elsewhere briefly summarised the uncertainty surrounding the phylogenetic position of *Scapter*, and the potential classificatory rearrangements stemming therefrom (Davies *et al.* 2005).

To facilitate morphological phylogenetic investigation of the colletids, we illustrate and discuss salient aspects of *Scapter* morphology. The morphology of the genus has only been superficially detailed in the literature to date. We also take the opportunity to describe three new species that have come to light, and evaluate the taxonomic status of several species described by Cockerell (1944a, b), which were inadvertently overlooked during Eardley's (1996) revision. The total of valid *Scapter* species now stands at 42.



Fig. 1. Dorsal view of female *Scapter bicolor*.

MATERIAL AND METHODS

Morphological terminology follows standard melittological references, e.g. Eickwort (1969: 338–374), Engel (2001: 19–33) and Michener (1944: 158–196, 2000: 40–52). Specimens for SEM examination were sputter-coated with gold-palladium and examined using a Phillips XL 30 ESEM at a working voltage of 10–15kV. Terminalia (of both sexes) were removed from relaxed specimens, immersed in cold 10% KOH for approximately 24 hours, neutralised with dilute acetic acid and rinsed in water. Terminalia were stored in microvials attached to the pin of the specimen.

Abbreviations used in this paper are: T – tergum (e.g. T1), S – sternum (e.g. S1), F – flagellomere (e.g. F1). In species descriptions, bilaterally symmetrical structures are described in the singular. The term *carinulate*, in describing surface sculpture, refers to largely parallel, longitudinal ridges packed fairly close together. In the species descriptions, the term *terminalia* has been used broadly to include T7–8 and sting (in ♀) and S6–8 and genitalia (in ♂). Measurements in the species descriptions largely follow the guidelines of Michener (2000, figs 10.3b, 10.8); head length is *sensu* Michener, i.e. top of vertex to ventral edge of clypeus and is not a longitudinal measurement.

Material examined was obtained from the following collections: Albany Museum, Grahamstown, South Africa (AMGS); Denis Brothers Private Collection, University of KwaZulu-Natal, Pietermaritzburg, South Africa (DJBC); Michael Kuhlmann Private Collection, University of Muenster, Germany (MKPC); Natural History Museum, London, United Kingdom (NHML); Natal Museum, Pietermaritzburg, South Africa (NMSA); South African Museum, Cape Town, South Africa (SAMC) and National Collection of Insects, Tshwane (formerly Pretoria), South Africa (SANC).

Engel (2005: 3–4) is followed in applying the rankless term Anthophila to the bee clade, a name that was commonly used for the bees in the nineteenth and early twentieth centuries. This clade name has already been adopted by other workers (e.g. Ohl & Bleidorn 2006).

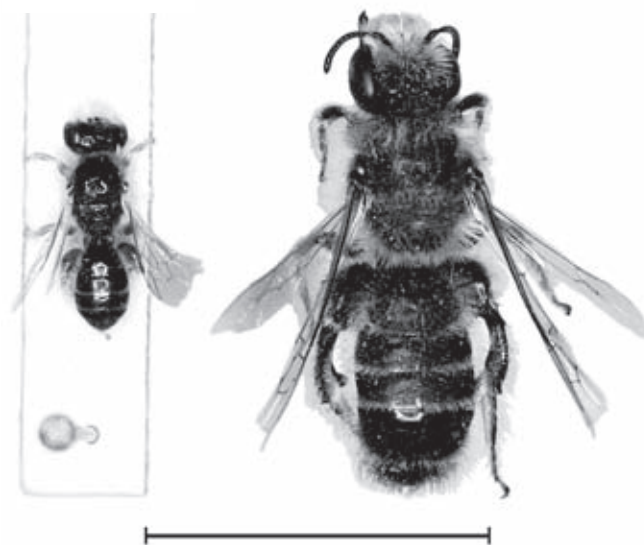


Fig. 2. Comparison of male *Scapter aureiferus* and male *S. heterodoxus*, showing size diversity in *Scapter*. Scale bar = 10 mm.

MORPHOLOGY

Description of Scapter

Three useful descriptions or diagnoses of *Scapter* now exist (Eardley 1996: 38–39; Michener 2000: 161–163; Ascher & Engel *in* Engel 2005: 13). All of these contain some inaccuracies, and thus a comprehensive description is provided here. Fuller information of variable characters (noted as ‘varied’) is provided in the section ‘Descriptive and Comparative Morphology’.

Body length 3.5–14 mm. Integument usually black or blackish. Legs frequently with yellow tarsomeres and tibia. Clypeus and paraocular areas never with any yellow maculation. Metasoma usually black; red or orange-red in some species. Integument never with metallic iridescence. Sexual dimorphism slight to pronounced, ♀ or ♂ may be the larger sex. Flagellum of female 10-segmented and male 11-segmented. Labrum varied. Single subantennal suture directed toward medial, lower margin of antennal socket (Fig. 3). Anterior tentorial pit located high on epistomal sulcus (Fig. 3). Malar area (space) absent (i.e. base of mandible articulates very close to ventral margin of compound eye). Mandibular structure varied. Facial fovea present in all taxa but shape varied. Lacinia present on dorsal margin of stipes, structure varied. Glossa short, subtruncate to weakly bilobed. Ventral (posterior) surface of prementum with fovea in both sexes. Galeal comb present, size not uniform. Postmentum a flat plate or a complex structure with lateral panels and posterior process. Maxillary palpi six-segmented, varied in length, some falling short of galea apex, others exceeding it. Labial palpi four-segmented. Cardo with inner process moderately produced (Fig. 4). Pronotum varied. Propodeum strongly angulate to declivitous. Surface of propodeal triangle varying from uniformly coriaceous to marked with carinae. Pre-episternal groove long extending to near the post-coxal process (Fig. 5). Female with brush on anterior (outer) side of probasitarsus, structure of hairs varied. Metabasitibial plate present in all taxa but form

varied. Female scopa from metatrochanter to metatibia, also on sterna. Long, simple keirotichia in female on metatibia. Arolia present. Pretarsal claws deeply cleft in male, variable in female (simple to cleft). Posterior (inner) metatibial spur in female ciliate (Fig. 6). Male metafemur and metatibia simple or with processes (armature). Metabasitarsus scarcely wider than following tarsomeres (metamediotarsus $0.95\times$ width of metabasitarsus). Two submarginal cells. Jugal lobe approximately $0.75\text{--}0.90\times$ length of vannal lobe. Anterior surface of T1 moderately concave with medio-longitudinal groove. Prepygidial fimbria present in females. Pygidial plate present in females and some males (Fig. 7). Fovea on sides of T2 (Fig. 8) present, absent in *S. tomentum* Eardley, 1996 and *S. albifumus* Eardley, 1996 and reduced in ♂ *S. heterodoxus* (Cockerell, 1921). Gradulus on T2 far removed from spiracle but not directed backward at the side (Fig. 8). No or two apicolateral lobes on male S7.

Descriptive and comparative morphology

Morphological features of *Scrapper* that show pronounced variation are discussed in more detail in this section. Furthermore, aspects of morphology that have featured prominently in colletid (and bee) literature are also examined. Brief comparative notes describing the structure in other colletid bees are appended to the end of each subsection (where relevant).

During our dissections, we were unable to identify any unambiguous shared, derived characters (synapomorphies) in all *Scrapper* species. In part, this is because of large gaps in knowledge of the detailed morphology of paracolletine, xeromelissine, euryglossine and hylaeine bees, which prevents confident identification of apomorphies for *Scrapper*. The question of whether *Scrapper* is a monophylum, thus, remains rather moot, although *pro tempore* it is defensible on traits that are not found in combination in other colletids, e.g. facial fovea, premental fovea, two submarginal cells, T2 fovea, hindleg and sternal scopae. McGinley (1981: 83) also identified a pronounced genal expansion posterior to the pleurostomal ridge in *S. niger* larvae, a characteristic ‘unlike all other known bee larvae’. This genal expansion is probably a *Scrapper* synapomorphy, but lack of *Scrapper* larvae makes it futile to pursue this point.

Labrum

The labrum is a small sclerite that articulates with the ventral edge of the clypeus. For practical reasons, we investigated the labrum in females only. The labrum is divided into two sections, an elevated, smooth, transverse, hairless *basal area* and a lower, hirsute *apical process* (Fig. 9). The sclerite is broader than long in all *Scrapper* species examined. The breadth:length ratio, however, varies greatly from 1.1:1 (i.e. sub-equal, e.g. *S. amplispinatus* Eardley, 1996; Fig. 10) to 3:1 (e.g. *S. bicolor* Lepeletier de Saint-Fargeau & Audinet-Serville, 1828; Fig. 11).

There is substantial variation on the basic conformation of the labrum. The type species, *S. bicolor*, is unique in the genus in having the *apical process* greatly reduced (Fig. 11). In some (e.g. *S. ruficornis* (Cockerell, 1916); Fig. 12; *S. flavipes* (Friese, 1925); Fig. 14) the apical process apex is constricted forming a small, narrow point (‘snout’), in others the apical process is broadly round to sub-truncate (e.g. *S. algoensis* (Friese, 1925); Fig. 13). The structure of the basal area also varies. The basal area may be greatly reduced (e.g. *S. flavipes*; Fig. 14). In some the basal area is bituberculate

(e.g. *S. albifumus*; Fig. 15). The anterior margin of the basal area is usually slightly pointed, sometimes sharply so (e.g. *S. chloris* Eardley, 1996; Fig. 16). A medial depression is often in evidence on the basal area (e.g. Figs 11–13, 16). The hairs on the apical process are always simple and tapering. The deployment of hairs on the apical process varies; they may be concentrated around the apical margins (e.g. *S. flavipes* Fig. 14), generally distributed across the apical process (e.g. *S. amplispinatus* Fig. 10) or concentrated in a longitudinal, medial band (e.g. *S. chloris* Fig. 16).

There is no thorough review of bee labra, and the treatment and illustration of colletid labra in the literature is patchy. In South American *Leioproctus* Smith, the apical area is frequently reduced (like *S. bicolor*) with the labrum being $>3\times$ as wide as long (e.g. Michener 1989, fig. 2e), although some have labra reminiscent of many *Scrapper* species (e.g. Michener 1989, fig. 6i). Why such variation occurs in this sclerite is unclear.

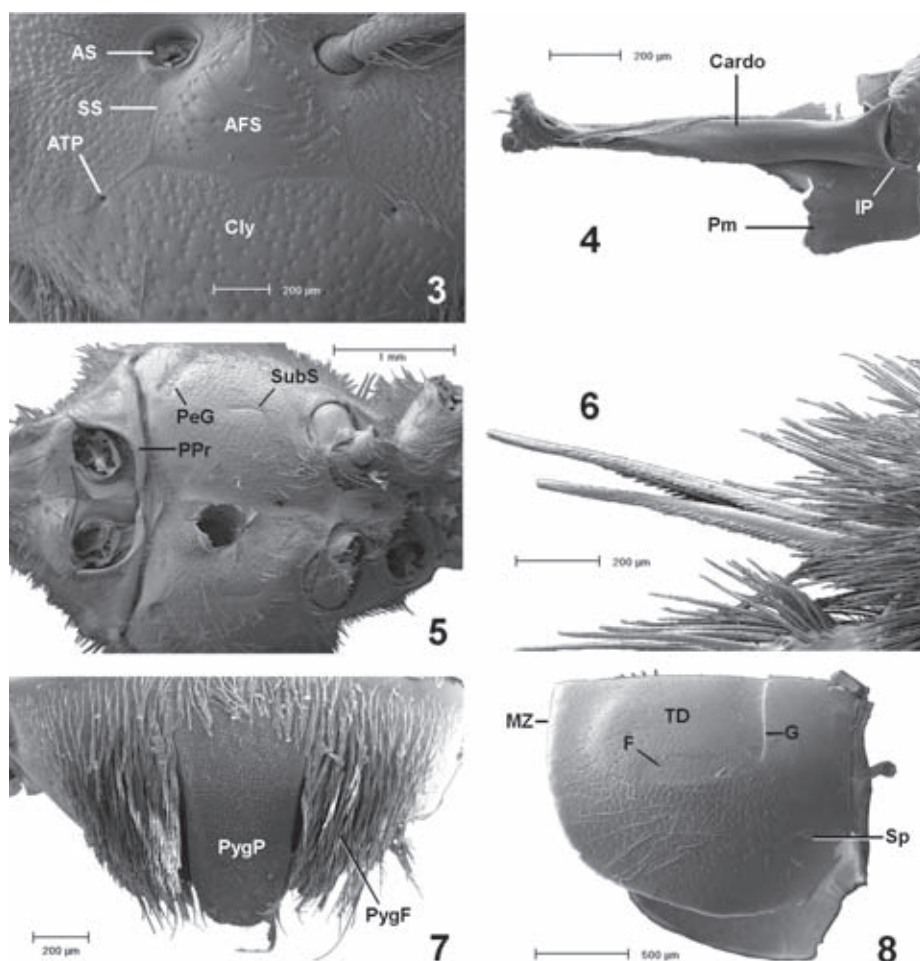
Glossa and paraglossa

The glossa in *Scrapper* conforms to the basic colletid type (McGinley 1980), which has to perform (in the female) two principal functions: (a) the loading and conveyance of nectar/pollen into the food canal, and (b) the application of the transparent membranous lining to the brood cells. In *Scrapper* the glossa is weakly bilobed (i.e. medially emarginate on the apical margin) to sub-truncate, approximately twice as wide as long and considerably shorter than the prementum (prementum $2\text{--}4.5\times$ as long as the glossa).

The glossa is divided into distinct sections (Fig. 17). Apically the *glossal brush* is borne on the *glossal lobes*, an extension of the *disannulate surface* (the ventral surface of the glossa). The *glossal brush* (Fig. 18) is dense with simple to branched hairs (the nature of the hairs is not easy to determine). The glossal lobes are narrow and separated from the remainder of the glossa by the *pre-apical fringe*, a distinct line of strongly compressed hairs. The *annulate surface* of the glossa takes up approximately $3/4$ of the glossa and consists of the *basiglossal sclerite* (which is undivided in *Scrapper*, Fig. 19), *pre-annular area* and *annular area*. The annular area (Fig. 20) is thickly covered in *glossal hairs*, which are deployed in approximately 10–20 tightly-packed, transverse rows or annuli. The hairs are sub-erect, spatulate, and, as described by Laroca *et al.* (1989) for *Niltonia* Moure (Colletinae *sensu* Michener), the lateral margins of these hairs are infolded and nearly touching, imparting a tubular nature to the basal part of the hairs. The glossa in *Scrapper* lacks clearly differentiated *basal* and *apical annular areas*, as also detected by McGinley (1980, fig. 9). The pre-annular area (Fig. 19) is comprised of approximately six rows of rather elongate, appressed, blunt-tipped hairs. At the pre-annular/annular area junction, the hairs are strongly flattened and compressed together. The *spiculate zone* of the pre-annular area is very restricted in *Scrapper*. We could not detect the *basiglossal sensilla* in our crude preparations, although McGinley (1980, fig. 9) illustrated them for '*Parapolyglossa paradoxa*' (= *Scrapper heterodoxus*).

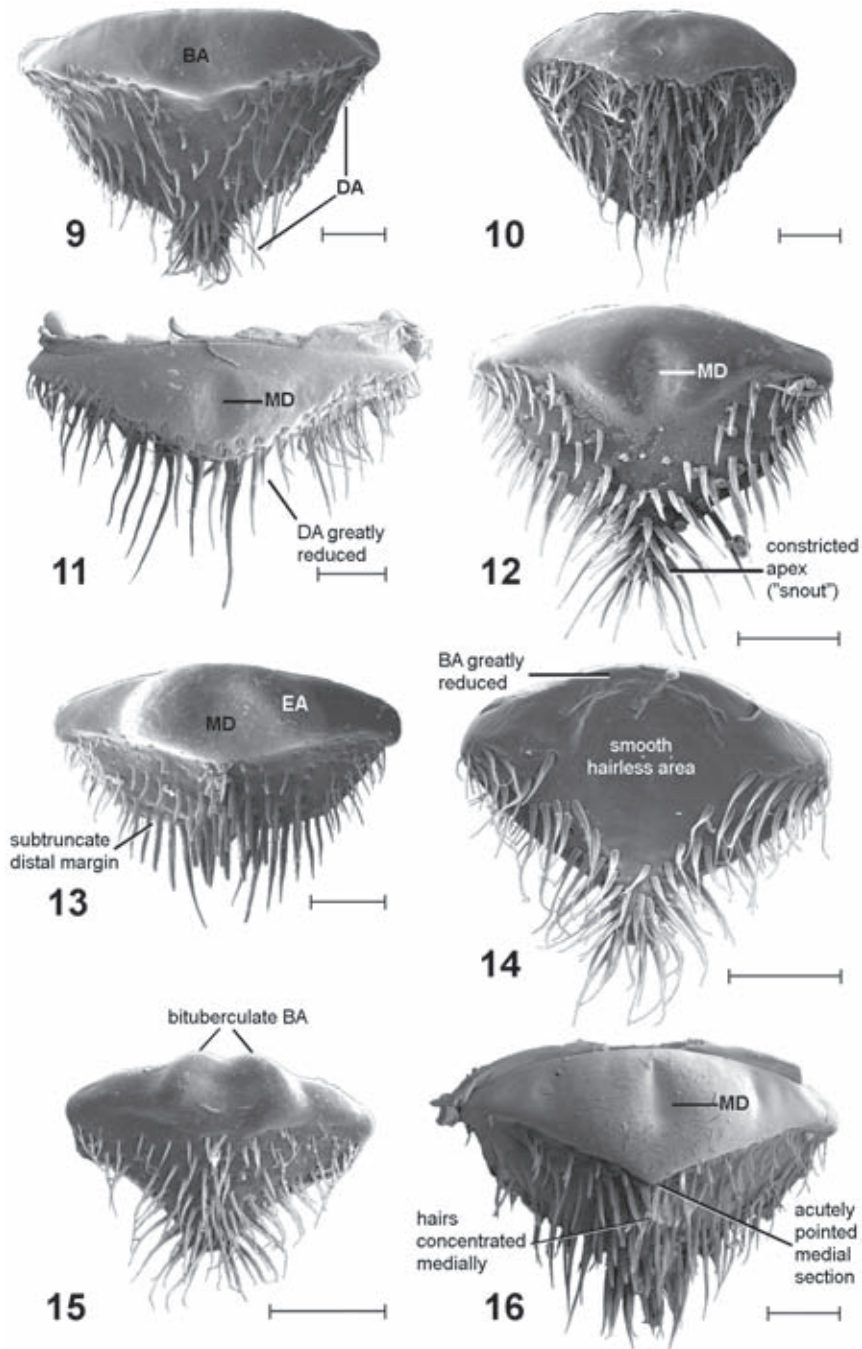
Overlapping and adjoining the basal and lateral portions of the glossa are the *paraglossae*. The *suspensorium of the paraglossa* is a large sclerite with a conspicuous row of approximately ten setae along the apical margin (Fig. 17). The paraglossa is elongate with a spatulate terminus and is hairy on the inner surface (Figs 17, 21).

The glossae of colletids have been studied by McGinley (1980), Michener and Brooks (1984) and Michener (1992), amongst others. McGinley (1980: 546) reported that glossal lobes are absent in the Euryglossinae. We examined one euryglossine exemplar



Figs 3–8. Morphological details of *S. chloris*: (3) Face, (4) Posterior view of cardo and postmentum, (5) Ventral view of mesosoma showing termination point of pre-episternal groove, (6) Metatibial spurs showing ciliate teeth, (7) Pygidial plate and pygidial fimbria, (8) Lateral view of T2 showing fovea. Abbreviations: AS – antennal socket, AFS – anterior face of supraclypeal area, ATP – anterior tentorial pit, Cly – clypeus, F – fovea, G – gradulus, IP – inner process, MZ – marginal zone, PeG – pre-episternal groove, Pm – postmentum, PPr – postcoxal process, PygF – pygidial fimbria, PygP – pygidial plate, Sp – spiracle, SS – subantennal suture, SubS – subpleural signum, TD – tergal disc.

(Fig. 22), and also found the glossal lobes greatly reduced (whether completely absent is more equivocal). If the absence or reduction of glossal lobes is true throughout the euryglossines, it may represent an apomorphy because clearly discernible glossal lobes are present in other colletids. Michener (1992, fig. 9) presented a hand-derived dendrogram (which he called a ‘summary of glossal characters’) of colletid relationships derived from nine binary glossal characters. *Scrapter* grouped with the ‘other Colletidae’ clade (composition of this clade not fully explained, but definitely including traditional Colletinae) that represented the sister-group to the Euryglossinae + Hylaeinae clade.



Figs 9–16. Labra of *Scapter* females: (9) *S. heterodoxus*, (10) *S. amplispinatus*, (11) *S. bicolor*, (12) *S. ruficornis*, (13) *S. algoensis*, (14) *S. flavipes*, (15) *S. albifumus*, (16) *S. chloris*. Abbreviations: BA – basal area, EA – elevated area, DA – distal area, MD – medial depression. Scale bars = 200 μ m.

The Euryglossinae + Hylaeinae clade was supported by a single character (annuli sharply segregated into basal and apical annular areas). As yet a satisfactory functional account for the operation of the colletid glossa has not been forthcoming. It is noteworthy that stenotritids (the apparent sister-group to the colletids, Danforth *et al.* 2006) lack a preapical fringe and glossal brush, and do not have the cellophane-like lining of the brood-cells characteristic of colletids. This suggests that the preapical fringe, glossal lobes and glossal brush are traits that evolved specifically for applying the brood-cell lining.

The morphology of the bee glossa and mouthparts, in general, has been extensively studied by melittologists. Indeed, proboscicial characters form a bulwark of many bee classifications and keys. By contrast, hymenopterists studying apoid wasps have devoted relatively little attention to mouthparts (e.g. the nugatory coverage in Bohart and Menke (1976)), and Ulrich's (1924) pioneering study (cited in Michener 1944) has no modern equivalent. This pronounced research asymmetry in the two sister-groups is worrying. As the phylogeny of bees is so sensitive to interpretations of glossal morphology (e.g. Series 1 vs Series 2 analyses in Alexander and Michener (1995)), an exhaustive modern survey of apoid wasp mouthparts is now an urgent requirement. An unpublished doctoral dissertation (Prentice 1998) apparently covers much of this ground (E.A.B. Almeida and M.S. Engel, *in litt.* 2006), but, as yet, no published papers have emerged from this study.

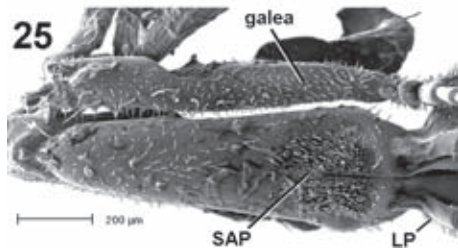
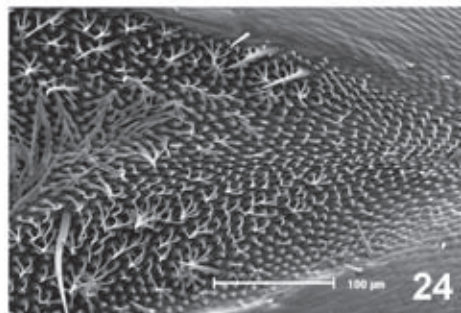
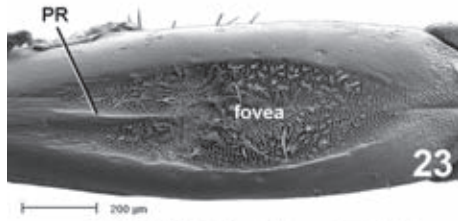
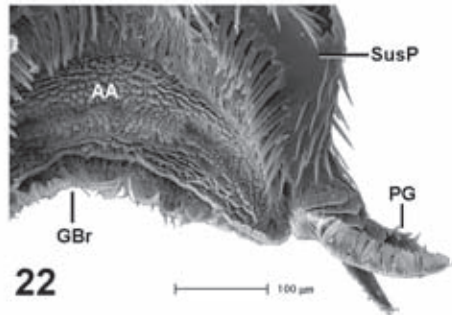
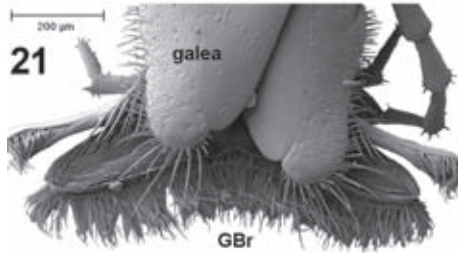
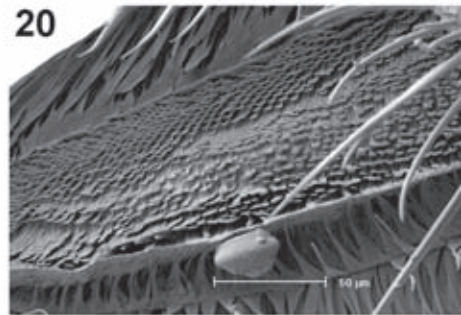
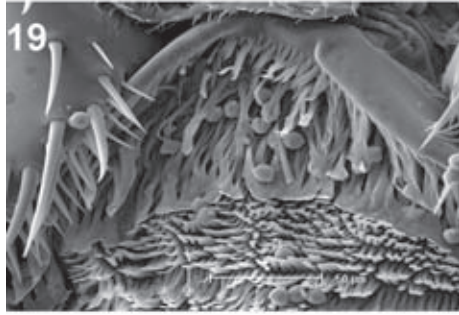
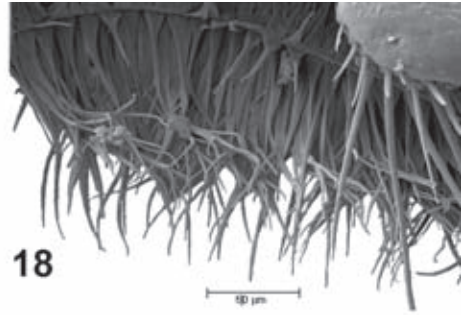
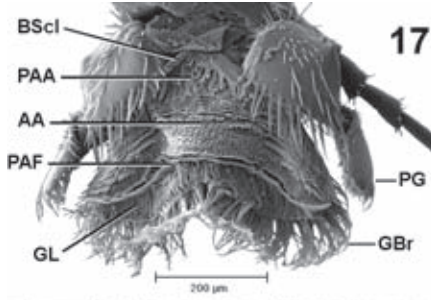
Prementum

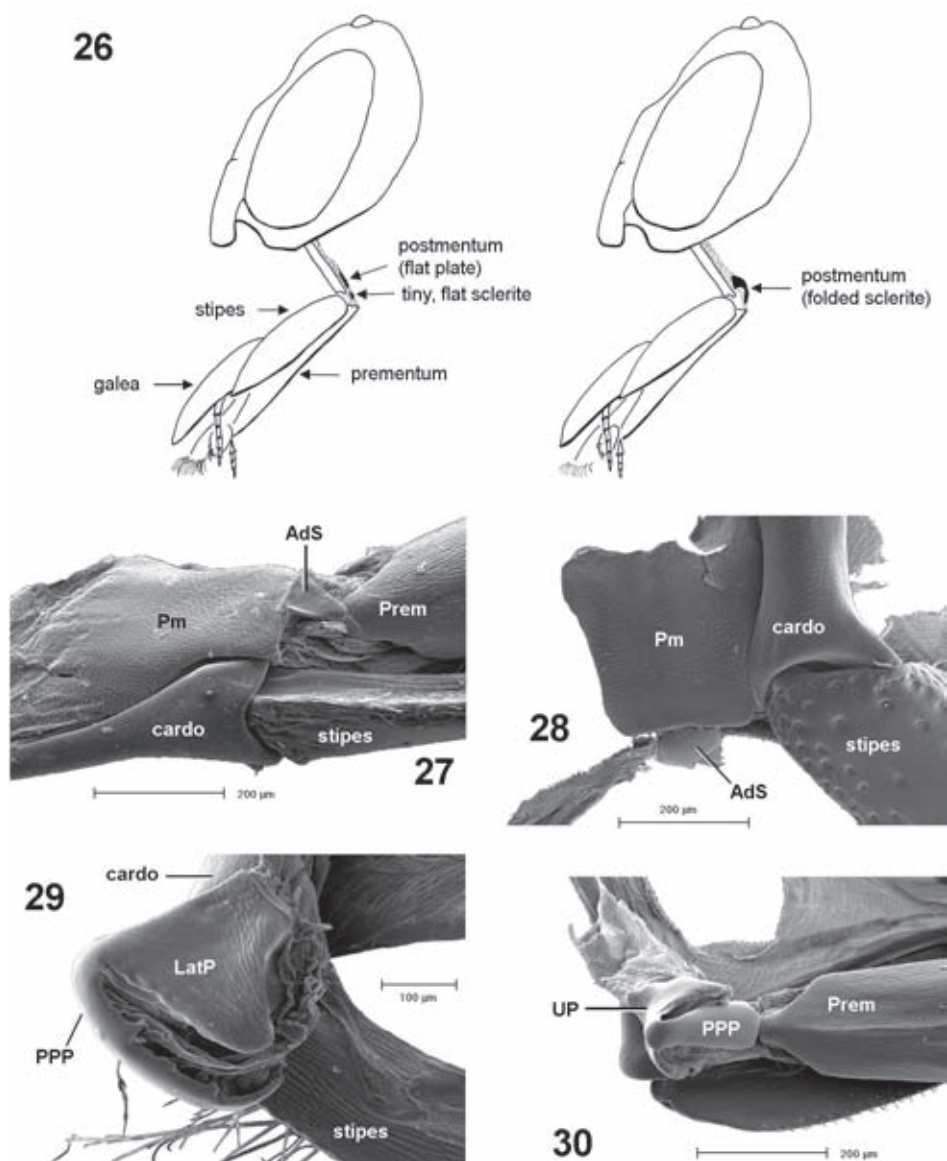
Both sexes of all *Scrapper* species have a fovea on the ventral (posterior) surface of the prementum (Fig. 23). The fovea is ovoid in shape and opens anteriorly onto the sublingual surface. Posteriorly a ridge extends into the basal third of the fovea. The fovea is densely packed with small spicules (Fig. 24). Although the length and breadth of the fovea varies in *Scrapper*, the structure of the fovea appears conservative in the group. The function of the fovea is unknown. A foveate prementum is absent in Colletinae (*sensu* Michener), but is found in hylaeines and xeromelissines (e.g. Michener 2000, fig. 38–19a), while euryglossines have a trend towards a spiculate fovea on the apical area of the prementum (Fig. 25).

Postmentum (= lorum and mentum *auct.*)

The terminology and homology of the basal sclerites of the bee labium have been the cause of substantial debate (reviewed in Plant & Paulus 1987). Essentially, the labium in bees comprises two sclerites—the apical, ligula-bearing sclerite (= *prementum*) and a basal sclerite occupying the space between the inner apices of the cardines and the base of the stipites (= *postmentum*) (Fig. 26). These sclerites are separated by a tough membrane, the *interscleritic labial membrane* (= ‘intersclerite membrane with

Figs 17–25. Details of mouthparts of *Scrapper* females and euryglossine bees: (17) Dorsal (anterior) view of *S. tomentum* glossa, (18) Glossal brush of *S. chloris*, (19) Pre-annular area and basiglossal sclerite of *S. tomentum*, (20) Pre-apical fringe and annular area of *S. chloris*, (21) Apices of galeae, glossa and paraglossae of *S. chloris*, (22) Dorsal (anterior) view of euryglossine glossa and paraglossa, (23) Ventral view of prementum of *S. chloris*, (24) Spicules in premental fovea of *S. chloris*, (25) Ventral view of prementum of euryglossine bee. Abbreviations: AA – annular area, BScl – basiglossal sclerite, GBr – glossal brush, GL – glossal lobe, LP – labial palpus, PAA – pre-annular area, PAF – pre-apical fringe, PG – paraglossa, PR – posterior ridge, SAP – spiculate area of prementum, SusP – suspensorium of paraglossa.





Figs 26–30. Details of mouthparts of *Scapter* bees: (26) Lateral view of mouthparts showing the two basic postmentum configurations, (27) Posterior view of postmentum and associated features of female *S. chloris*, (28) Posterior view of postmentum and cardo of female *S. algoensis*, (29) Lateral view of postmentum of female *S. amplispinatus*, (30) Oblique posterior view of postmentum and associated structures of female *S. nitidus* (note that the posterior process of postmentum has been artificially pushed into contact with the premental apodeme). Abbreviations: AdS – additional sclerite, LatP – lateral ‘panel’ of postmentum (= ‘lorum’), Pm – postmentum, PPP – posterior process of postmentum, Prem – prementum, UP – upper part of postmentum.

mesocuticular outline' of Plant and Paulus (1987)). The basal sclerite (= *postmentum*) may be subdivided in some bees into two different sclerites, which Winston (1979: 641) and Michener (1984, 2000) have termed the *lorum* and *mentum*. Plant and Paulus (1987) restricted use of these terms to the Apinae (*sensu* Michener 2000), and argued that distinct lora and menta were absent in other bees. We consider the arguments of Plant and Paulus (1987) correct.

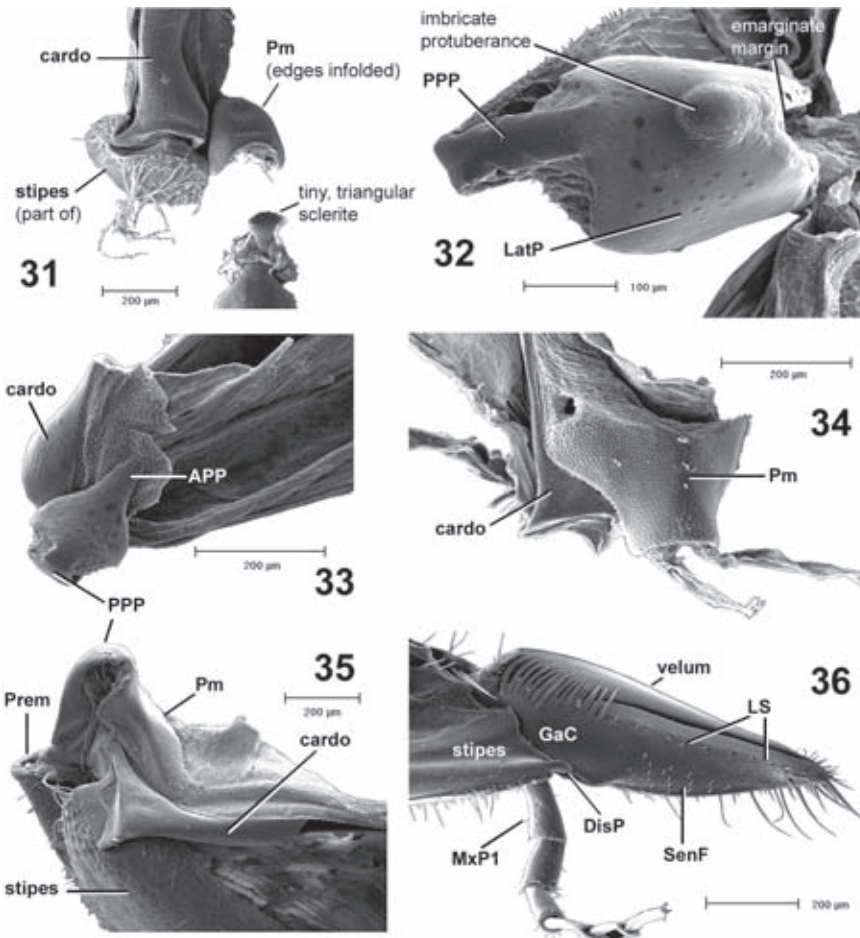
In *Scrapper* two different basal-sclerite arrangements are observed (Fig. 26): (1) a flat plate between the apical ends of the cardines linked by the tough interscleritic labial membrane to the basal apodeme of the prementum, with the interscleritic membrane enclosing a tiny sclerotised plate (Figs 27, 28); and (2) a sclerite composed of two, lateral 'panels' that are joined medially and lie between the ends of the cardines (this arrangement can be envisaged as a flat sclerite that has become strongly infolded), postero-ventrally a narrow process curls forward below the halves and is separated by the interscleritic labial membrane from the prementum (Figs 29, 30). In other words, in the first arrangement, three separate sclerotised pieces can be distinguished (prementum + tiny, often triangular plate + larger, flat, sometimes sub-quadrate plate), whereas, in the second arrangement, only two sclerotised pieces can be seen (prementum + infolded sclerite with process).

We are cautious to apply specific terminology to these basal sclerites, but the most plausible interpretation is that, in both arrangements, there is a single basal sclerite (i.e. the postmentum) and that in (1) the interscleritic labial membrane has developed a weak, medial, sclerotised section (a secondary development). Using Michener's (1984) approach, the tiny sclerotised piece in the membrane would be interpreted as a true mentum. The mentum is, however, a subdivision of the postmentum, whereas state (1) in *Scrapper* appears to be the scleritisation of the interscleritic membrane and not the subdivision of the postmentum. Ergo, the triscleritic complex of some *Scrapper* species is only convergently similar to the superficially similar state seen in the Apinae (Plant & Paulus 1987, figs 13–16).

An apparently intermediate condition between the two states is observed in *S. bicolor* (recall, the type species of the genus). Here the sclerite between the cardine apices is moderately infolded and not a flat plate; but it is still separate from the small, triangular sclerite adjacent to the prementum (Fig. 31).

In those *Scrapper* species with state (2) there is variation in the structure of the dorsal portion of the sclerite. In *S. heterodoxus* the apical margin is emarginate and a protuberance that has squamous patterning is visible on the postero-dorsal surface (Fig. 32). In *S. caesariatus* Eardley, 1996 there is an additional dorsal process protruding from the apical margin (Fig. 33).

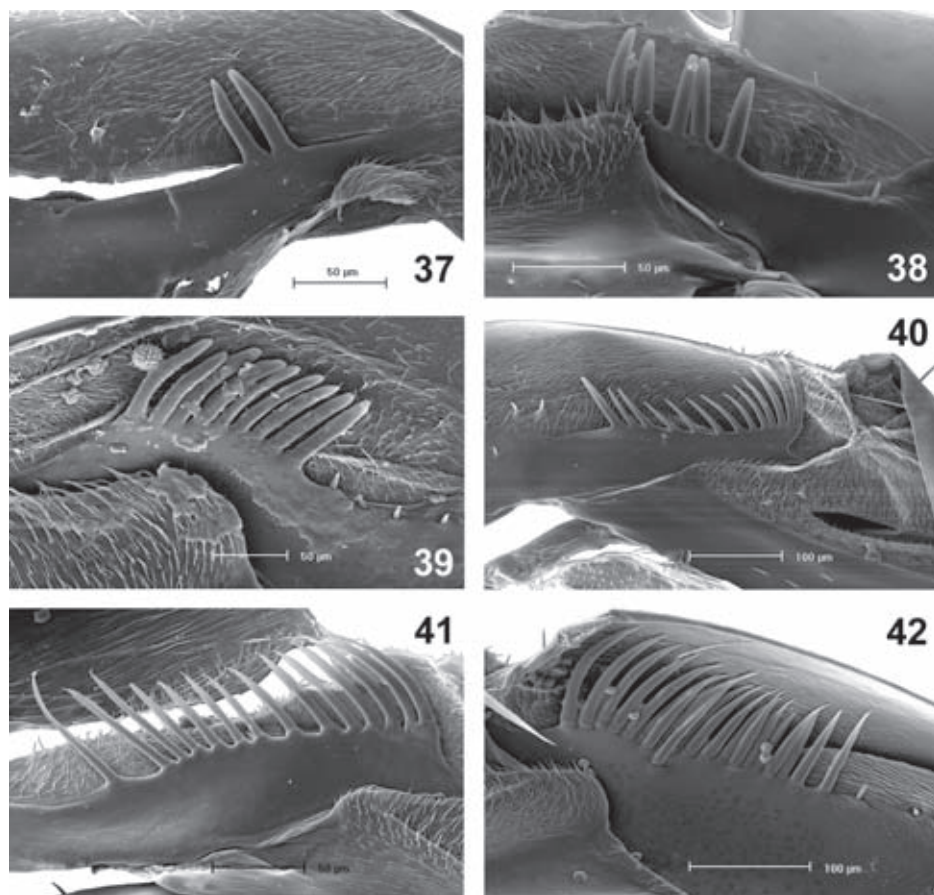
In Hylaeinae, Xeromelissinae and Euryglossinae the postmentum is a small, flat, usually sub-quadrate plate (Fig. 34; Michener 1944: 209, 1984: 709–710, figs 11–16; Plant & Paulus 1987: 86, fig. 2). The postmentum is separated from the prementum by the interscleritic labial membrane. Michener (1984: 709–710) interpreted the membrane to be a non-sclerotised mentum. The condition in the hylaeines and euryglossines is similar to state (1) described above for certain *Scrapper* species, with the exception that those scrapperines always have a part of the interscleritic labial membrane sclerotised. This *Scrapper* condition can easily be derived from that in the euryglossines and hylaeines, or vice versa. The postmentum in euryglossines, hylaeines and xeromelissines



Figs 31–36. Details of mouthparts of colletid bees: (31) Posterior view of postmentum and associated structures of female *Scapter bicolor*, (32) Dorsal view of postmentum of female *S. heterodoxus*, (33) Oblique dorsal view of postmentum of female *Scapter caesariatus*, (34) Posterior view of postmentum of euryglossine bee, (35) Lateral view of postmentum of *Paracolletes* species, (36) Inner view of galea of female *Scapter tomentum*. Abbreviations: APP – anterior process of postmentum, DisP – dististipital process, GaC – galeal comb, LatP – lateral ‘panel’ of postmentum, LS – line of sensilla, MxP1 – maxillary palpus 1, Pm – postmentum, PPP – posterior process of postmentum, Prem – prementum, SenF – sensory field.

resembles that of apoid wasps (e.g. Plant & Paulus 1987, figs 20–23), and such a postmentum was argued to be the plesiomorphic condition for bees by Plant and Paulus (1987: 96–97, fig. 29). GBPD agreed with this interpretation (plausibly making the euryglossines-hylaeines the most plesiomorphic bee lineage); but such a viewpoint is not in agreement with Danforth *et al.* (2006), who suggest that dasypodaine melittids rather than colletids are the most plesiomorphic bee clade.

In the Colletinae (*sensu* Michener 2000, excluding *Scapter*), the postmentum is a well-sclerotised body with a narrow extension or process that curls underneath the basal section and is attached to the interscleritic labial membrane (Fig. 35; Michener 1984:



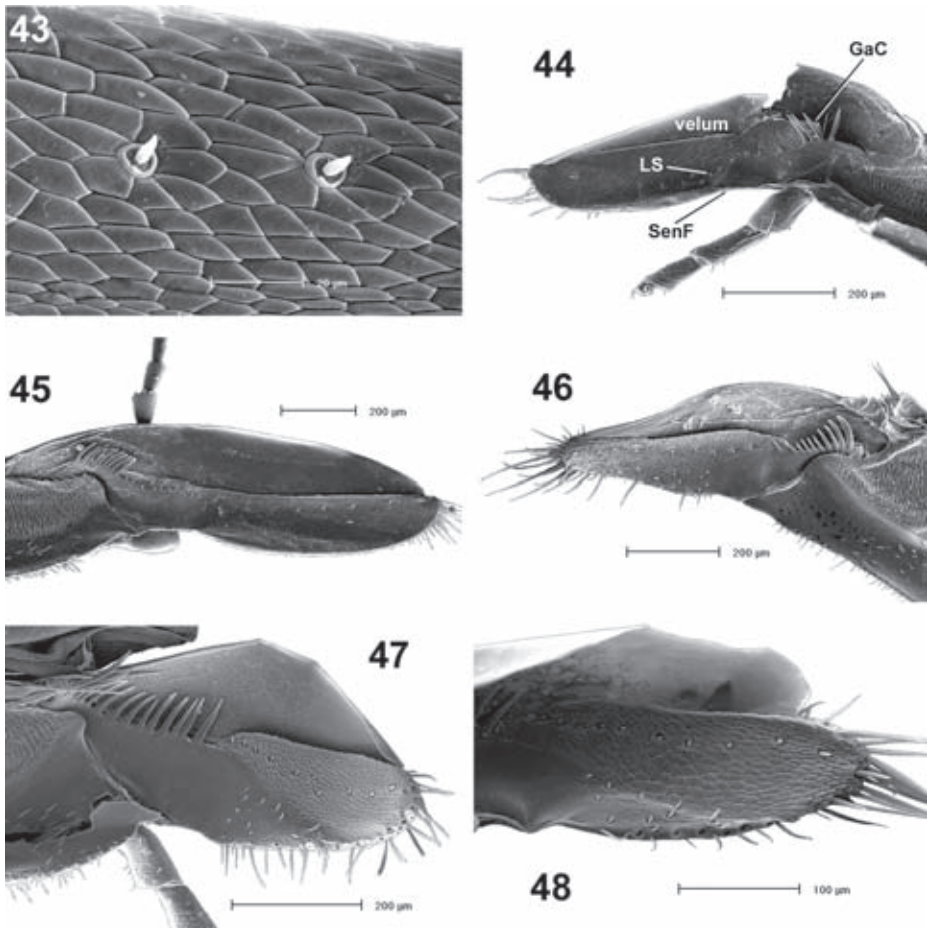
Figs 37–42. Galeal comb of *Scrapper* bees: (37) *S. nitidus*, (38) *S. aureiferus*, (39) *S. heterodoxus*, (40) *S. caesariatus*, (41) *S. albifumus*, (42) *S. tomentum*.

710, figs 17–20; Plant & Paulus 1987: 87–88, fig. 5). This condition agrees closely with state (2) described above for certain *Scrapper* species, and is illustrated for an unspecified *Scrapper* species by Michener (1984, figs 21, 22), although an unsclerotised gap putatively separated the dorsal sclerite ('lorum') and posterior process ('mentum') in Michener's preparation. However, in our dissections, those *Scrapper* species with a state (2) postmentum, the dorsal sclerite and posterior process are not separated. It is in state (1) that a three sclerite condition is observed.

The disparity in the structure of the postmentum of *Scrapper* was an unexpected discovery. Such a marked difference weakens belief in the monophyly of the genus. A thorough survey of the postmentum of as many colletid genera as possible (particularly of Australian and South American paracolletines) may cast further light on the evolution of the colletid postmentum.

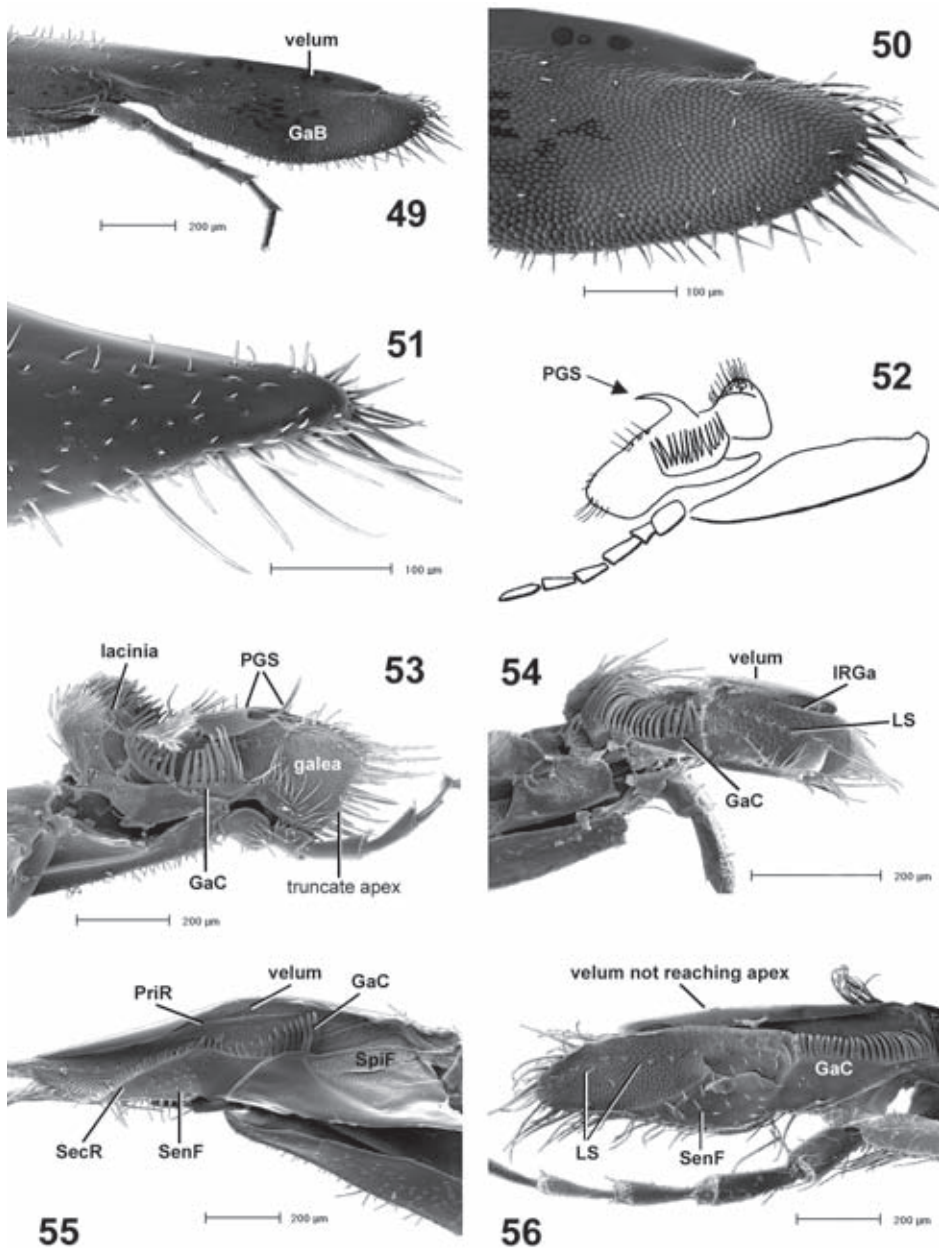
Galea

The galea is the thin, apical-most sclerite of the maxilla. On its slightly concave inner surface, there is a row of bristles ('teeth') called the *galeal comb* arising on the



Figs 43–48. Galeal structures in *Scapter*: (43) Sensilla from sensillar line in *S. amplatarsus*; (44–48) Inner view of galea of females: (44) *S. flavipes*, (45) *S. heterodoxus*, (46) *S. amplatarsus*, (47) *S. algoensis*, (48) *S. absonus*. Abbreviations: GaC – galeal comb, LS – line of sensilla, SenF – sensory field.

base of the *inner rib of the galea* (Fig. 36). *Scapter* has universally been held to have a small galeal comb consisting of fewer than five teeth (Cockerell & Ireland 1933: 973; Michener 2000: 127, 161; Ascher & Engel in Engel 2005: 13), although Friese (1909, fig. 19) illustrated *Polyglossa capensis* (= *S. capensis* (Friese, 1909)) with a comb of approximately 15 teeth. Dissections for this study have revealed a range of comb sizes in the group. The number of teeth varies from 2 to 20 (Figs 37–42), and plotting all the values available as a bar graph shows a smooth continuum without any gaps. The teeth are generally slightly procurved and may be of equal length or increase in length basally. The teeth may be acuminate or rather blunt (compare Figs 45, 46). The galeal comb is used to clean pollen off the forelegs (Jander 1976: 188–189; Krenn *et al.* 2005: 26). There does not seem to be a clear correlation between the size of the galeal comb and the nature of the anterior probasitarsal brush hairs (cf. Jander 1976: 188–189). For example, both *S. flavipes* and *S. tomentum* have anterior probasitarsal brushes composed



Figs 49–56. Details of maxillae of colletid bees: (49) Outer view of galea and maxillary palp of female *Scrapper amplispinatus*; (50, 51) Outer view of galeal apex of *S. amplispinatus* and *S. tomentum* females respectively; (52) Inner view of maxilla of euryglossine bee showing procurved galeal spine; (53–56) Inner view of galea: (53) euryglossine bee, (54) hylaeine bee, (55) *Colletes* species (note the primary and secondary ribs), (56) *Leioproctus* (*Lamprocolletes*) species. Abbreviations: GaC – galeal comb, IRGa – inner rib of galea, LS – line of sensilla, PGS – procurved galeal spine, PriR – primary rib, SecR – secondary rib, SenF – sensory field.

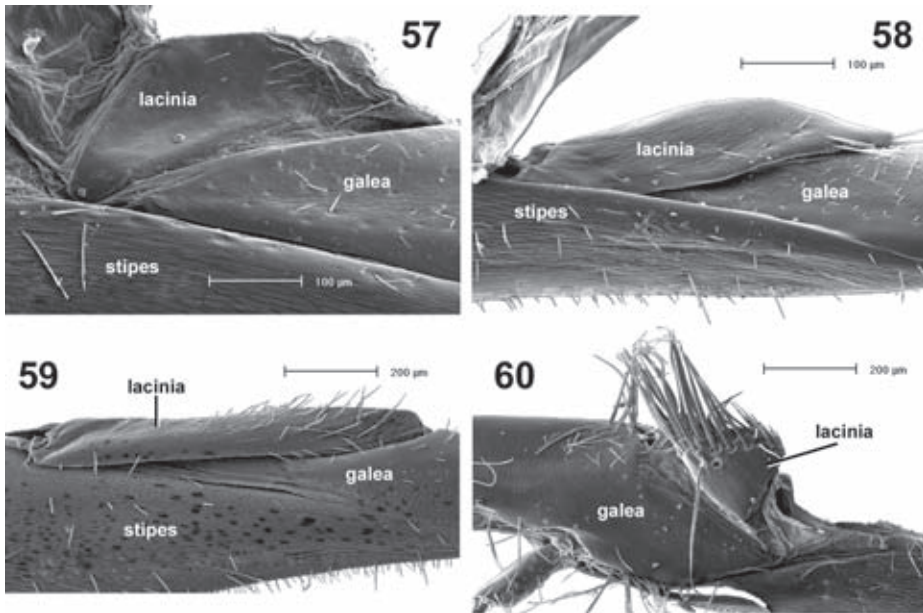
of simple hairs, yet *flavipes* has a small comb (approx. 4 teeth) whereas *tomentum* has a large comb (approx. 20 teeth).

There is a *line of sensilla* running parallel to the inner rib of the galea extending from the end of the galeal comb to the apex of the galea (Figs 36, 43). These sensilla are found in all *Scapter* species. On the ventro-medial section of the galea is the *sensory field* (Fig. 36) composed of sensillae similar to those in the sensillar line. The shape of the sensory field varies from species to species, and is greatly reduced in some (e.g. *S. flavipes*; Fig. 44).

All *Scapter* species possess the *galeal velum* (Fig 36). This is the thin, uppermost partition of the galea. There is notable variation in the outline of the velum: strongly tapering (*S. tomentum*; Fig. 36), weakly convex (*S. heterodoxus*; Fig. 45), convex but emarginate apically (*S. amplatarsus* (Friese, 1913); Fig. 46), strongly convex (*S. algoensis*; Fig. 47), broadly-rounded but falling short of the galeal apex (*S. absonus* Eardley; Fig. 48) and narrow and largely parallel-sided (*S. amplispinatus*; Fig. 49). The external surface of the galea below the galeal velum varies in surface sculpturing. In many *Scapter* species the surface is squamous (Fig. 50), but some have a smooth surface with no trace of roughening (Fig. 51).

Although significant attention has been given to bee glossal structure, the maxilla of 'short-tongued bees' has received far less treatment. The euryglossine galea (Figs 52, 53) is strongly divergent from that of *Scapter*. The apex is abruptly truncate, the velum is absent, and there is a distinctive, acuminate appendage on the dorsal edge of the basal part of the galea, here named the *procurved galeal spine* (term suggested by M.S. Engel). Furthermore, the galeal comb stands apart from the main galeal sclerite on a robust, crescentic sclerite that is also connected to the sensory field area. The hylaeine galea is similar to that of euryglossines (Fig. 54), but the velum is present and procurved galeal spine absent. The hylaeine galeal comb is also on a strong crescentic sclerite that is not closely contiguous with the inner galeal rib. In xeromelissines the galeal comb is reportedly quite weak, consisting of 10 or fewer teeth (Michener 2000: 171). Other features of the xeromelissine galea are unknown to us. In a *Colletes* Latreille exemplar, from Lesotho, we observed that there are two separate ribs on the inner galeal surface (Fig. 55). The first (primary) rib divides the velum from the rest of the galea. The second (secondary) rib separates the galeal comb and sensory field from the main galeal sclerite. The galea of *Colletes* could be thought of as comprising three sclerites: (1) the lower-most, smooth, galeal comb-bearing sclerite; (2) the main galeal sclerite with squamous patterning; and (3) the velum. It is unclear whether this tripartite galea is universal in *Colletes*, or that we merely chose an unusual exemplar; this requires verification. The galea in paracolletines such as *Leioproctus* (*Lamprocolletes* Smith) and *Paracolletes* Smith is similar to that of *Scapter*: the velum is present, and the galeal comb is closely associated with the inner galeal rib (Fig. 56). The galeal comb appears fairly well developed in most paracolletines with approx. 10–20 teeth (e.g. Fig. 56; Rayment 1954, figs 7, 8; Houston 1990, fig. 3i; Michener 2000, fig. 38–18a).

Interpretation of the diverse colletid galeae is not easy. A possible transformation series exists leading from the triscleritic condition of *Colletes* to the euryglossines/hylaeines (where the lowest sclerite bearing the galeal comb and sensory field has become partially associated with the main galeal sclerite), and finally *Scapter* and the para-

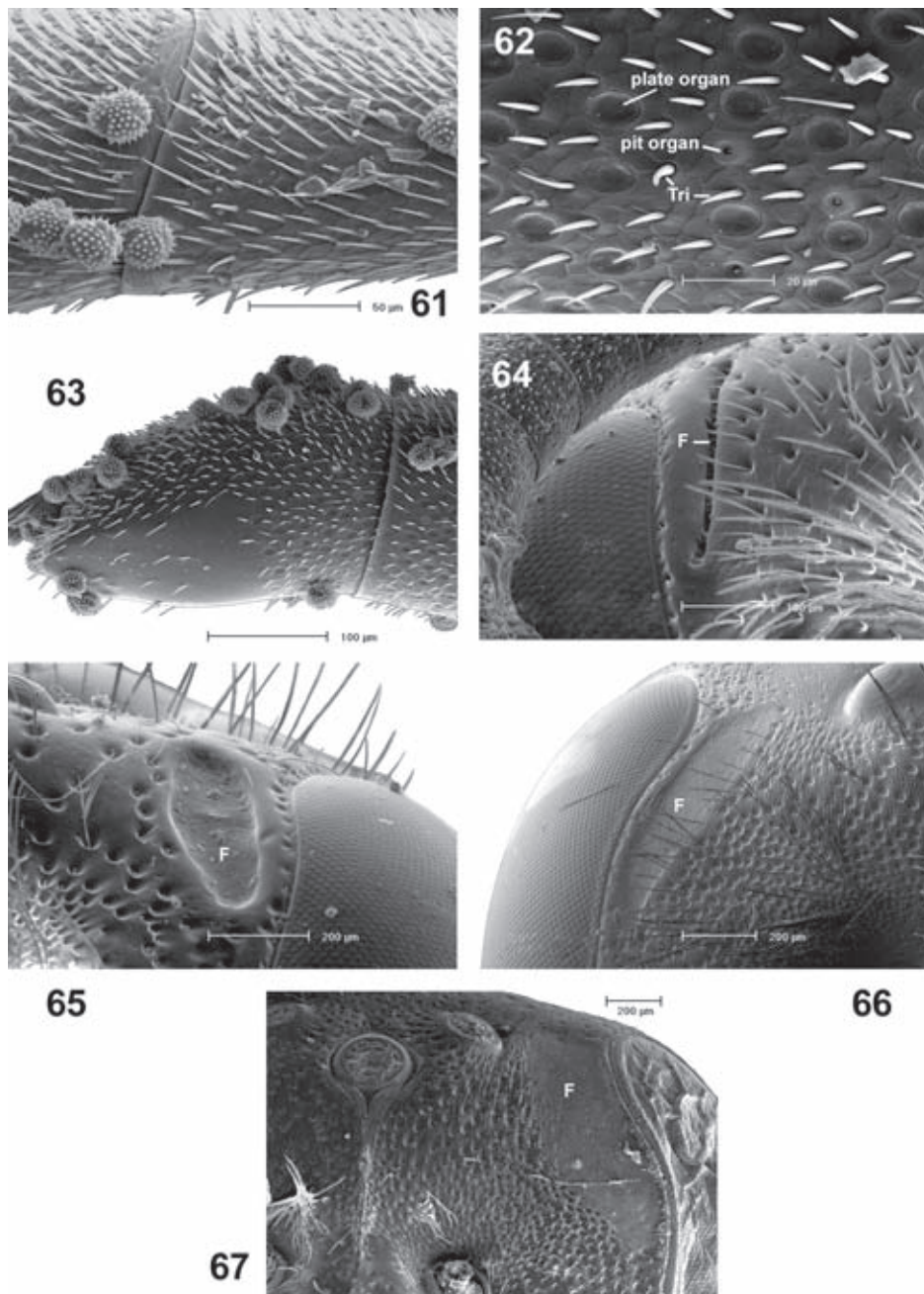


Figs 57–60. Outer view of laciniae of colletid females: (57) *Scrapter chloris*, (58) *S. nitidus*, (59) *S. amplispinatus*, (60) *Leioproctus* (*Lamprocolletes*).

colletines (where the lowest sclerite is completely attached to the main galeal sclerite and only distinguishable by its smooth surface), or vice versa. We can only invite melittologists, especially those studying colletids, to subject the galeae of their study objects to SEM investigation.

Lacinia

We examined the lacinia in only four *Scrapter* species, but the variation shown was noteworthy. The lacinia in three species (*S. nitidus* (Friese, 1909), *S. chloris* and *S. bicolor*) was an irregularly-shaped, weakly squamous to smooth sclerite, widest medially and tapering at the ends and positioned on the postero-dorsal margin of the galea and dorsal margin of the stipes (Figs 57, 58). The lacinia in *S. amplispinatus* was notably different being an elongate, largely parallel-sided sclerite (Fig. 59). The laciniae of colletids (and other bees) have been little described or illustrated in the literature. The laciniae in euryglossines and hylaeines are fairly large (in relation to galea), robust sclerites with strong setae; noticeably different from *Scrapter*. The lacinia in xeromelissines is described as a weakly-developed, almost hairless, elongate sclerite along the dorsal margin of the galea or stipes (Michener 1995: 333), but we are unaware of further details. In the paracolletine *Leioproctus* (*Lamprocolletes*), we observed that the lacinia is a roughly triangular, smooth sclerite with strongly developed setae on the apical margin (Fig. 60). *Colletes* apparently lacks the lacinia altogether (Michener 1944: 208; Stephen *et al.* 1969: 9), which may be an apomorphic loss if true throughout that huge genus. A comprehensive SEM study of colletid laciniae would probably be a productive exercise.



Figs 61–67. Flagellomeres 1 and 2 (61), 9 (62) and 10 (63) of female *Scapter nitidus*, and facial foveae of *Scapter* females (64–67): (64) *S. nitidus*, (65) *S. basutorum*, (66) *S. chloris*, (67) *S. bicolor*. Abbreviations: F – fovea, Tri – trichoid sensillae.

Antennal sensilla

Ågren (1977, 1978), Ågren and Svensson (1982) and Ågren and Hallberg (1996) have comprehensively investigated the different types of sensilla found on the flagellomeres of bees. The distribution and conformation of these sensilla appears to be generally conservative across the bee clades and, hence, relatively uninformative from a phylogenetic perspective.

As far as we are aware, however, the antennal sensilla have only been documented for two genera of colletids, viz. *Colletes* and *Hyaleus* (Ågren 1977). To flesh out the corpus of data, a brief description is provided here for female *Scrapper* bees.

The basal flagellomeres are thickly covered in sharp, simple setae (Fig. 61). From about F6 onwards, *plate organs* (*sensilla placodea*) become evident, as do occasional *pit organs* and *sensilla campaniformia*. The plate organs vary subtly in outline from circular to oval (Fig. 62) and are depressed medially. The pit organs are sunken circular features with a central hole bearing a slightly protruding, peg-like structure (Fig. 63). A variety of *trichoid sensilla* are present on the apical flagellomeres (Fig. 63). These range from long (15 µm), thin hairs (approximately 15× longer than broad) to shorter (5–8 µm), stubbier hairs (approximately 5× longer than broad). Ågren (1977, 1978) and other authors have divided trichoid sensilla into different types, but classification is not easy and we have merely termed them trichoid sensilla. On the final flagellomere (F10), there is a largely naked zone disto-ventrally (Fig. 63). Such a bare area is observed in other colletids (Ågren 1977) and andrenids (Ågren 1978).

Facial fovea

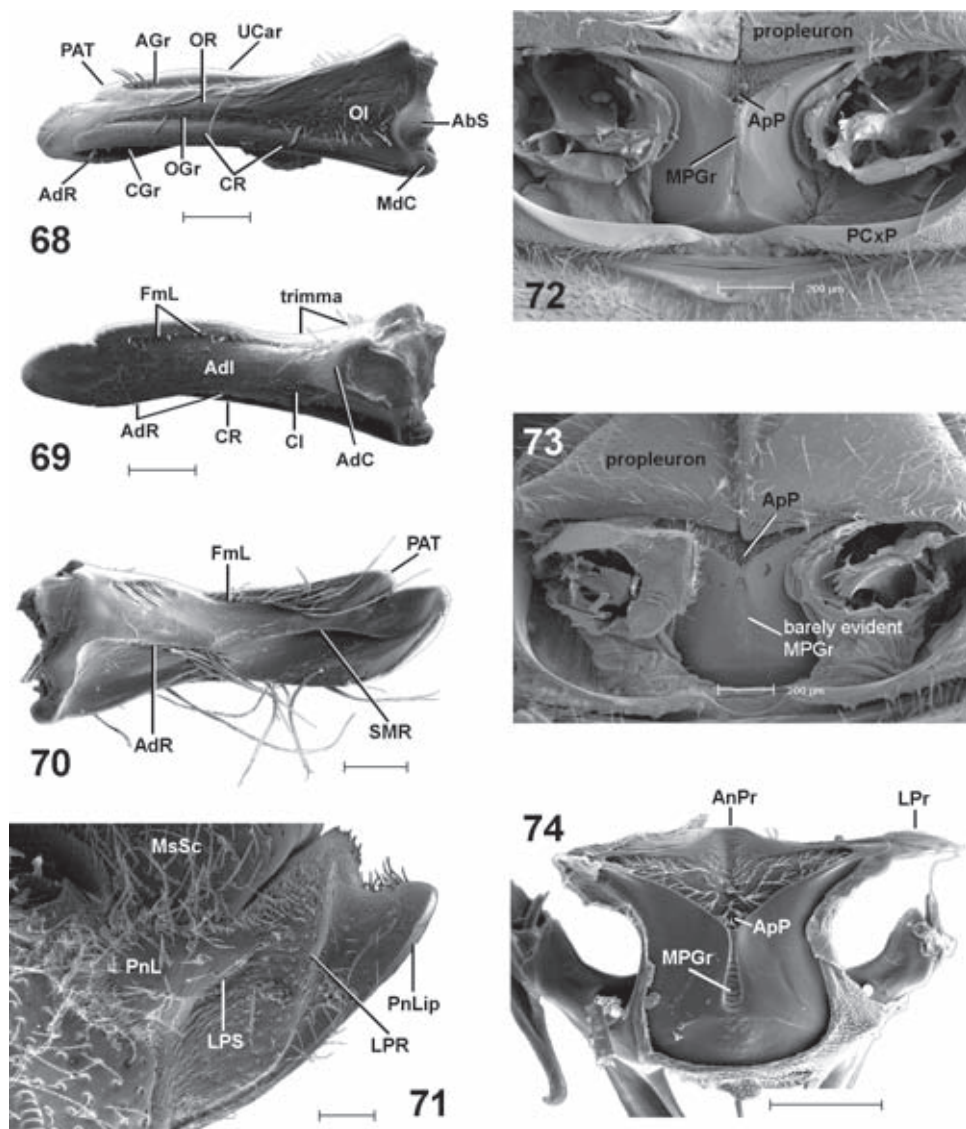
Schönitzer and Schuberth (1993) and Schuberth and Schönitzer (1993) have investigated the morphology of facial foveae in bees. They reported a facial fovea in the upper paraocular area in most 'short-tongued' bees, with an epithelial gland below the fovea (Schönitzer & Schuberth 1993, figs 10, 11). The fovea was found to be more strongly developed in females than males. Earlier, Houston (1975: 7) described facial foveae in Australian hylaeine bees, and detected 'what appeared to be secretory epithelium underlying a porose area of cuticle'. Exactly what is secreted from these facial foveae remains unknown.

In *Scrapper* a fovea is present in all species (and both sexes), but there is considerable variation in its appearance. In some species (e.g. *S. nitidus*, Fig. 64) there is a deep, narrow groove beginning slightly dorsad of the upper eye margin and running obliquely to about 1/3 down the length of the eye. The bottom of the groove cannot be seen and there are no hairs in the groove. These facial foveae have a strong similarity to those of Hylaeinae and Euryglossinae (e.g. Houston 1975, fig. 28; Schönitzer & Schuberth 1993, fig. 6; Exley 1996, figs 2–5). This trait is also reported in paracolletines like *Callomelitta* Smith and some *Eulonchopria* Brèthes (Michener 1965: 36; 1989: 669, 670; 2000: 162).

In other species (e.g. *S. basatorum* (Cockerell, 1915)) the fovea forms a fairly well-defined ovoid bowl with smooth surface and no hairs (e.g. Fig. 65), or shallow with squamous patterning (e.g. *S. chloris*, Fig. 66), or indistinct, broad and poorly differentiated from the surrounding integument (e.g. *S. bicolor*, Fig. 67).

Mandible (Figs 68, 69)

Michener & Fraser (1978) have extensively reviewed the mandibular structure of bees. In this study only the mandibles of female *Scrapper* species were investigated.



Figs 68–74. Details of mouthparts and thorax of female *Scapter* and *Colletes* bees: (68, 69) Outer and inner views of left mandible of *S. algoensis*, (70) Inner view of left mandible of *Colletes* species, (71) Lateral view of pronotum of *S. nitidus* showing lateral pronotal ridge, (72) Prosternum of *S. chloris*, (73) Prosternum of *S. bicolor*, (74) Prosternum of *S. nitidus*. Abbreviations: AbS – abductor swelling, AdC – adductor convexity, Adl – adductor interspace, AdR – adductor ridge, AGr – acetabular groove, AnPr – anterior process, ApP – apophyseal pit, CGr – condylar groove, CI – condylar interspace, CR – condylar ridge, FmL – fimbriate line/groove, LPR – lateral pronotal ridge, LPr – lateral process, LPS – lateral pronotal sulcus, MdC – mandibular condyle, MPGr – median prosternal groove, MsSc – mesoscutum, OGr – outer groove, Ol – outer interspace, OR – outer ridge, PAT – pre-apical tooth, PCxP – postcoxal process, PnL – pronotal lobe, PnLip – pronotal lip, SMR – secondary, median ridge, UCar – upper carina. Scale bars = 200 µm.

The *Scrapter* mandible fits what Michener & Fraser (1978: 474) term the ‘ancestral type of [bee] mandible’ that is found in most ground-nesting bees (colletids to fideliids).

In *Scrapter* there is a single *pre-apical* (*sub-apical*) tooth. The *acetabular groove* is present (a few hairs in the groove), ventrally the *acetabular groove* is separated from the narrow, deep *outer groove* by the smooth *outer ridge*. The *outer ridge* curves upwards basally. The outer groove opens basally where it becomes the *outer interspace*. The outer groove generally has many long, downward-curved, simple hairs that become much shorter on the outer interspace. The apex of the *outer groove* extends apically slightly further than the apex of the acetabular groove. The outer groove is separated from the *condylar groove* by the smooth, hairless *condylar ridge*. The condylar ridge forms the ventral-most edge of the mandible for most of its length and basally joins the *mandibular condyle*. In the apical-most portion of the mandible, the *adductor ridge* curls round from the inner surface to terminate on the cap of the rutellum and thus constitutes the ventral-most edge of mandible apically. The *condylar groove* begins on the lower inner surface of the mandible but extends onto the outer surface anteriorly separating the condylar and adductor ridges. Apically the condylar groove extends weakly beyond an imaginary line dropped from the pre-apical tooth.

The inner surface of the mandible is dominated by a large basal swelling, the *adductor convexity* (Fig. 69). The lower edge of the convexity is represented by the adductor ridge. Ventrally, the *condylar interspace* separates the adductor and condylar ridges. A line or shallow groove is present near the upper margin of the inner surface and is called the *fimbriate line*. Above the adductor convexity is the *trimma*, a gently sloping area covered in short hairs. No clearly defined *trimmal carina*, separating the trimma and adductor convexity, is evident in *Scrapter*.

Within the Colletidae, the ‘ancestral mandible’ is observed in *Colletes* (Michener & Fraser 1978, fig. 2), paracolletines and Diphaglossinae (Michener & Fraser 1978: 474). The status in Euryglossinae is not discussed in Michener and Fraser (1978). Contrasting with other colletids, the twig- and cavity-nesting Hyaelinae and Xeromelissinae have modified mandibles. They are sub-triangular (i.e. broad at the base, tapering strongly to the apex) with an extremely broad *outer interspace* (Michener & Fraser 1978, fig. 5). These modifications presumably relate to their nesting habits. We are unaware of the mandibular structure in ground-nesting xeromelissines such as *Geodiscelis* Michener & Rozen. Michener and Rozen (1999: 3) merely reported (in *G. megacephala*) that the female has a ‘strong pre-apical tooth’, and Packer (2005: 88) observed that the female of *G. longiceps* has a ‘small pre-apical tooth’. Michener and Fraser (1978: 474) described ‘a broad, secondary, longitudinal median ridge in the adductor interspace’ of the inner mandibular surface in *Colletes* (Fig. 70), *Amphylaeus* Michener and *Callomelitta* (weakly developed). This ‘special and doubtless derived ridge’ (Michener & Fraser 1978) is not seen in *Scrapter*.

Pronotum

Eickwort (1969: 344, fig. 30), McGinley (1986: 11, figs 9–12) and Engel (2000: 17–18, figs 30, 31) have investigated pronotal ridges in halictid bees. We are unaware of any detailed treatment of pronotal ridges in colletid bees. There is notable variation in the development of ridges and sulci on the pronotum in *Scrapter*.

The *lateral ridge of pronotum* begins on the dorsal surface of the pronotum and terminates on the sides of the pronotum (Fig. 71). The ridge is prominently developed and sharp-edged in some taxa (e.g. *S. tomentum*, *S. calx* Eardley, 1996), to weakly defined (e.g. *S. chloris*) or completely absent (e.g. *S. amplitarsus*) in others. A strong groove, the *lateral pronotal sulcus*, begins near the lateral ridge, runs obliquely down the side of the pronotum terminating near the mesepisternum (Fig. 71). The lateral pronotal sulcus marks off the *pronotal lobe* distinctly.

Prosternum

The prosternum is partly hidden ventrally by the procoxae and propleura. Three *Scapter* species were examined, and some variation was encountered. In *S. bicolor*, *S. chloris*, and *S. nitidus* the *apophyseal pit* is largely hidden (Figs 72–74). The *median prosternal groove* is long and conspicuously pitted in *S. nitidus*, less strongly developed in *S. chloris* and is barely evident in *S. bicolor*. The *lateral processes* are long in *S. chloris* and *S. bicolor* (Figs 72, 73), but shorter in *S. nitidus* (Fig. 74). We are unaware of any detailed examination of prosterna in colletid bees (or bees in general). A detailed investigation of the pro- and endosternum in bees would probably provide many points of phylogenetic value to melittologists.

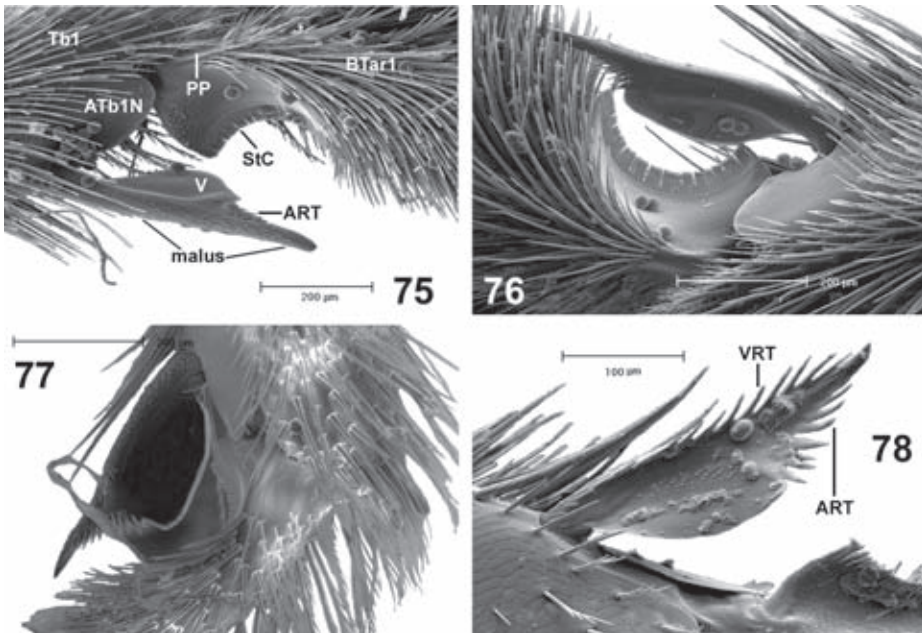
Antenna cleaner (= strigilis)

Schönitzer (1986) has reviewed the structure of the antenna cleaner or strigilis in bees. The antenna cleaner is composed of two parts (Fig. 75): (1) the *strigilar concavity*, a comb-bearing notch on the postero-basal section of the probasitarsus, and (2) the *malus*, a modified protibial spur. The malus consists of a thin, lamellate *velum* and a narrow, often squamous *trunk* that terminates apically in the *apex* (Fig. 75). A short row of seven to nine teeth (*apical row of teeth*) is present on the anterior edge of the apex (Fig. 75). The apex is about 0.3–0.6× the length of the trunk. The velum is broadest apically and tapers basally. The apical edge of the velum varies in *Scapter*; it may be rounded (e.g. *S. amplispinatus*; Fig. 76), sharply pointed (e.g. *S. bicolor*; Fig. 75) or truncate (e.g. *S. capensis*; Fig. 77). The trunk is covered in pointed squamae, but varies from being weakly (e.g. *S. amplispinatus*) to thickly covered (e.g. *S. bicolor*). On the postero-ventral margin of the malus is the *ventral row of teeth* (Fig. 78). This row is variably developed in *Scapter*: the teeth are near-absent in some taxa (e.g. *S. chloris*) to well-developed in others (e.g. *S. nitidus*).

There is little literature on antenna cleaners in colletids. Schönitzer (1986, figs 1, 2) illustrated two species of *Hylaeus* Fabricius (= *Prosopis* Fabricius), that showed pronounced intra-generic variation. The *Scapter* antenna cleaner is similar in general terms to that illustrated for *Hylaeus*. Schönitzer (1986: 47) averred that a plesiomorphic ('ancestral') antenna cleaner is characterised by a slender velum, long apex, squamous trunk and two rows of teeth. Most of these traits are displayed by *Scapter* (and other colletid bees).

Pollen-collecting and grooming brushes

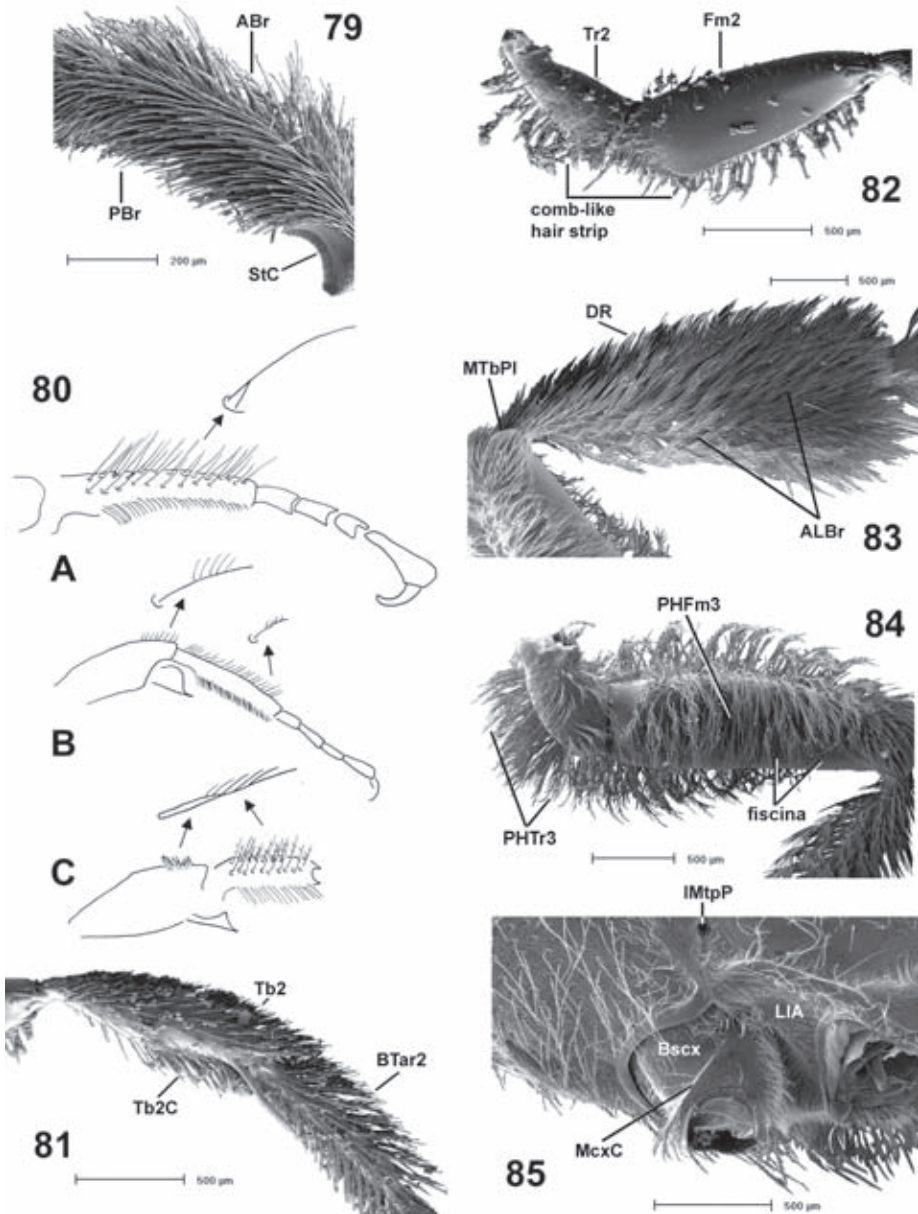
All *Scapter* species of both sexes have *pro-*, *meso-* and *metabasitarsal posterior brushes*. These are dense brushes composed of short, simple hairs, presumably for general grooming, on the underside of the basitarsi (Fig. 79). There was no detectable variation in the structure of these brushes in *Scapter*. The brush hairs agree with Braue's



Figs 75–78. Antenna cleaners of *Scrapper* females: (75) *S. bicolor*, (76) *S. amplispinatus*, (77) *S. capensis*, (78) *S. flavostictus*. Abbreviations: ART – apical row of teeth, ATb1N – apical protibial notch, BTar1 – probasitarsus, PP – probasitarsal pit, StC – strigilar comb, Tb1 – protibia, V – velum, VRT – ventral row of teeth.

‘Bürstenhaare am ersten Tarsenglied’ (Braue 1913: 86, figs 5, 6). Jander (1976: 187) described an ‘oblique furrow within the [posterior mesobasitarsal] brush’ in certain diploglossine colletids. Such furrows were not observed in *Scrapper*.

On the anterior side of the probasitarsus there is another brush (Figs 79, 80). Eickwort (1969: 349) used the term *anterior probasitarsal brush* specifically for a row of flattened setae on the outer edge of the probasitarsus in augochlorine halictids. This brush is not homologous with the brush seen in *Scrapper* and, hence, we refrain from using Eickwort’s term, positionally descriptive as it is (perhaps Eickwort’s halictid brush should be renamed the *anterior probasitarsal pecten*, leaving the other term for more general use). The structure of the scrapperine brush varies. Some species have brushes comprising only simple hairs (e.g. *S. basutorum*; Fig. 80A), others only branched hairs (e.g. *S. heterodoxus*, *S. bicolor*; Figs 80B, 80C) and still others a combination of both (e.g. *S. luridus* Eardley, 1996). The diversity in structure of these brushes suggests a difference in function, presumably related to scraping pollen off the anthers (e.g. Michener *et al.* 1978: 581; Houston 1990: 589, 2000; Michener 2000: 15; Müller & Kuhlmann 2003), or perhaps the cleaning of the underside of the head (Jander 1976: 183). Therefore differences in the structure of the anteriorly-positioned probasitarsal brush may be related to flower preferences (flower/pollen structure) rather than any phylogenetic signal. The antero-apical portion of the protibia also has the same type of branched hairs (in those species bearing branched hairs), and is a continuation of this brush. The branched hairs present in these brushes approach Braue’s group of ‘Einseitig, gefiederte Haare’ (Braue



Figs 79–85. Legs structures of *Scapter* bees: (79) Probasitarsal brushes of female *S. absonus*; (80) Lateral view of extended forelegs showing probasitarsal brushes: (A) *S. basatorum*, (B) *S. bicolor*, (C) *S. heterodoxus*; (81) Mesotibial comb of *S. nitidus*; (82) Mesotrochanter and mesofemur of *S. nitidus*; (83) Metatibial scopa of *S. bicolor*; (84) Fiscina of *S. bicolor*; (85) Mesocoxa of *S. bicolor*. Abbreviations: ABr – anterior brush, ALBr – antero-lateral brush of softer, palmate hairs, Bscx – ‘basicoxite’, BTar2 – mesobasitarsus, DR – dorsal ridge of stout, branched hairs, Fm2 – mesofemur, IMtpP – inferior metapleural pit, LIA – lateral intercoxal area, MxC – mesocoxal carina, MTbPI – metabasitibial plate, PBr – posterior brush, PHFm3 – plumose, pollen-holding hairs of metafemur, PHTr3 – plumose hairs of metatrochanter, StC – strigilar comb, Tb2 – mesotibia, Tb2C – mesotibial comb, Tr2 – mesotrochanter.

1913: 89, figs 19 or 23). In females with brushes bearing branched hairs (e.g. *S. heterodoxus*), the males have simple hairs (supporting the notion that these brushes are for pollen-collection).

In South American *Leioproctus*, Michener (1989: 632) reported that the 'front basitarsus of female usually without well formed comb of hairs on outer margin, but such a row of hairs present in subgenera *Cephalocolletes*, *Nomiocolletes*, *Reedapis*, and *Spinolapis*'.

On the mid leg, *Scrapter* has a strip of hair on the postero-apical section of the mesotibia, which is the *mesotibial comb* (Fig. 81). Jander (1976: 187) restricted the term to the Halictidae and Andrenidae, noting 'on the mesotibia of Colletidae no conspicuous brush or comb is found'. Michener (2000: 48), Engel (2001: 35) and others have used the term 'mesotibial comb' more broadly. The *Scrapter* mesotibial comb is appreciably less pronounced than that seen in halictids (GBPD pers. obs.). Opposing the mesotibial comb and mesobasitarsal posterior brush is a comb-like strip of hair on the proximo-ventral part of the mesofemur and mesotrochanter (Fig. 82). Thus, a mesotrochanter-mesofemur/mesotibial-mesobasitarsal coupling is achieved for the cleaning of the foreleg (see Jander 1976: 184–186 for discussion).

Pollen is packaged into scopae on the hindlegs and also on the sterna in *Scrapter*. The pollen grains packaged into the scopae are always dry i.e. never moistened with nectar. The *hindleg scopa* is most strongly developed on the metatibia, where a thick mass of plumose hairs is present. The metatibial scopa is divided into two sections (Fig. 83): a dorsal ridge of dense, stout, branched hairs (near fig. 23 of Braue (1913)) and an antero-lateral swathe of long, softer, palmate hairs (near figs 25, 26 of Braue (1913)). The antero-lateral section represents the primary pollen-holding hairs. Stockhammer (1966: 183–184) observed that the dorsal serrated and claw-like (simple, curved) hairs on the metatibia of ground-nesting augochlorine halictids serve as support 'when the tibiae are pressed against the walls of a tunnel'. His observations suggest that the dorsal ridge of stiffer hairs (where pollen is more weakly represented) in *Scrapter* may have an additional (or different) function to the softer, antero-lateral hairs, i.e. they may serve as aids to the crampon-like metabasitibial plate in navigating nest tunnels. On the posterior face of the metatibia are simple, longish hairs, which are the *keirotrichia* ('shorn hairs'). Short keirotrichia are widespread in bees and wasps, but Michener (1989: 628) suggested long keirotrichia may be an apomorphy for the paracolletine genus *Leioproctus*. Keirotrichia are apparently used to clean the wings (Michener 2000: 48; see also Jander & Jander 1978).

The anterior part of the metafemur has a curtain of long, plumose hairs, hanging downward (Fig. 84). These hairs abut a naked, smooth area that lies on the antero-ventral side of the metafemur and is the 'corbicula' of Michener (2000: 130), or more precisely the *fiscina* (Engel 2001: 28).

The metatrochanter has a ventral fringe of long, plumose hairs (the branches are concentrated apically on each hair and approach hairs in fig. 23 of Braue (1913)), and evidently it forms part of the functional scopa (Fig. 84). The metacoxa also has a ventral fringe of soft, minutely plumose bristles, but the hairs are different from those of the metatrochanter, and the metacoxal hairs do not form part of the functional scopa. The metabasitarsus has the usual grooming brush posteriorly. Antero-dorsally it has a few, curved, stiff, branched hairs, but these are of feeble importance for the scopa. Thus, in

summary, the scopa in *Scapter* on the hindleg is (in terms of importance): metatibia + metafemur + metatrochanter (+ metabasitarsus).

An important ancillary part of the scopa on all *Scapter* species is the presence of plumose hairs on the sterna. The branched hairs are conspicuous and fairly dense on S2, while being sparser on S1 and S3–4. These hairs are ventrally-directed with three to five side-branches per seta. In foraging females, these sternal hairs (especially on S2) are always heavily packed with pollen. That the sternal hairs are ‘scopal’ is also indicated by the absence of plumose hairs on the sterna in males. Alexander and Michener (1995, character 93) coded a sternal scopa as absent in *Scapter* (using *S. heterodoxus* as their exemplar), but this is incorrect. A sternal scopa is also found in some South American paracolletines (Michener 1989: 630) and Australian *Leioproctus* species (Houston 2000: 9, figs 11–14).

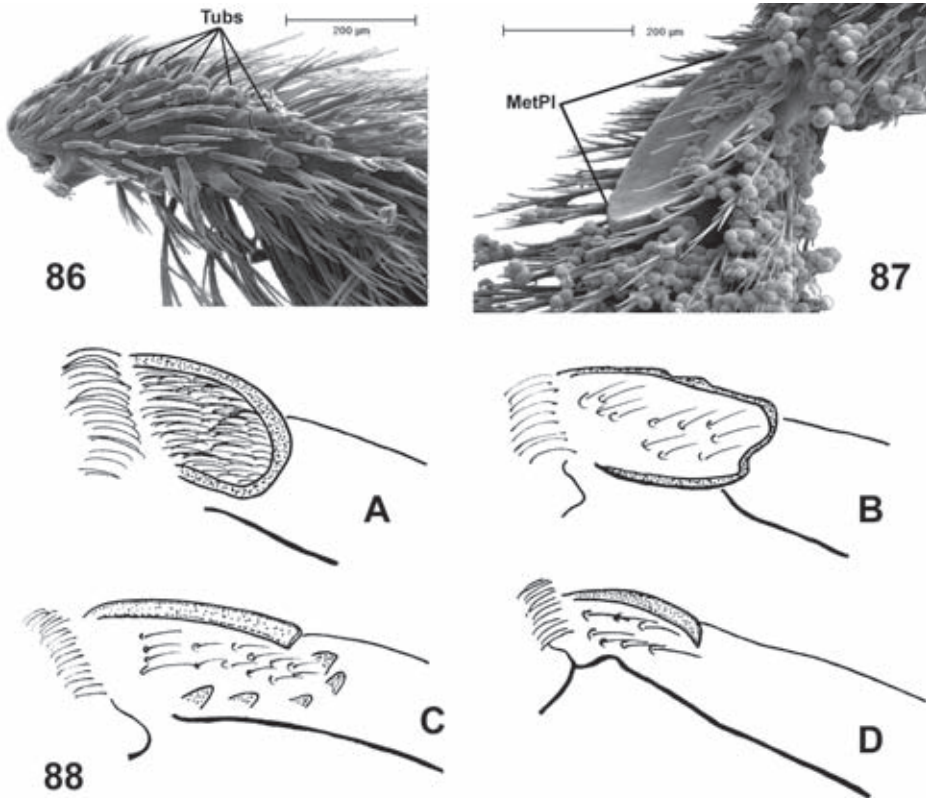
Scopae are absent in euryglossines and hylaeines which transport pollen internally (the hairs on the metatibiae are simple in these bees, excluding the apical metatibial ‘penicillus’). There have been few dedicated studies on scopae in scopa-bearing colletid bees. Pasteels and Pasteels (1976) investigated the colletid scopae using scanning electron microscopy. They emphasised the diversity of scopal types in the colletids, and re-affirmed the belief that the nudity of hylaeines and euryglossines was secondarily derived, because they presumed scopae would be ineffectual in tiny bees: ‘...rappelons que ce sont des insectes de petite taille, chez lesquels une scopa formée d’une couverture de soies ne serait probablement pas efficace’ (Pasteels & Pasteels 1976: 99). Their treatment was rather generalised, and *Scapter* approaches most closely the scopae described for the Colletinae (e.g. Pasteels & Pasteels 1976, figs 18–20). Michener (1989, fig. 19) illustrated representative hairs from the ‘lower part’ of the metatibial scopa in South American paracolletines. The scapterines most resemble the tibial hairs illustrated for *Leioproctus* subgenus *Peditomorpha* Ashmead and, to a lesser extent, *Leioproctus sensu stricto*; these taxa having apically-concentrated side-branches, usually restricted to one side of the seta.

Mesocoxa

Michener (1981) studied the mesocoxae of bees (and some ‘sphecids’), and found that the mesocoxa of bees forms a vertically elongate spindle divided into two unequal halves: a large *basicoxite* and a small *disticoxite*. The bees were also divided into two groups: those with hemicryptic mesocoxae (i.e. most of basicoxite withdrawn under the pleuron) and those with mostly exposed mesocoxae. Melo (1999: 18) showed that the basicoxite is absent in bees and apoid wasps, but did not propose any new terminology for the divided coxa. Within the colletid clade, all groups have a hemicryptic mesocoxa with the putative exception of the euryglossines and xeromelissines (Michener 1981: 321); this characterisation was reversed in Alexander and Michener (1995) where the exemplars were coded as having a partially hidden mesocoxa (character 71). In *Scapter* the mesocoxa is hemicryptic with a fairly strong *mesocoxal carina* (Fig. 85).

Metabasitibial plate

The metabasitibial plate lies on the dorso-basal area of the metatibia and is used for gaining purchase while the bee moves along the tunnels of the nest or fashions the brood chambers (Batra 1964; Stockhammer 1966: 183; Michener 2000: 32, 48).

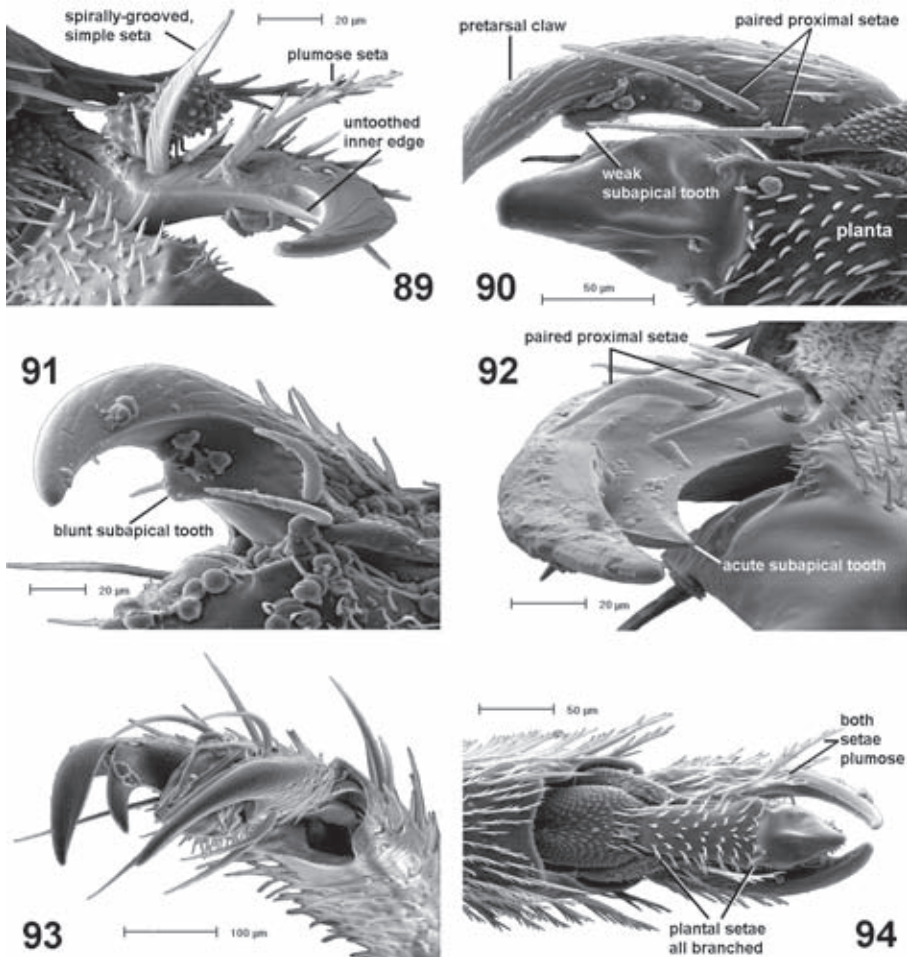


Figs 86–88. Metabasitibial plates of *Scrapper* bees: (86) female *S. pruinus* sp. n.; (87) female *S. nitidus*; (88) Anterior view of metabasitibial plates: (A) female *S. armatipes*, (B) male *S. capensis*, (C) female *S. tomentum*, (D) male *S. algoensis*. Abbreviations: MetPl – metabasitibial plate margin entire, Tubs – tubercles delimiting edge of metabasitibial plate.

Differences in metabasitibial plate structure may, therefore, relate to differences in nesting substrate.

The metabasitibial plate varies greatly amongst *Scrapper* species. All *Scrapper* species (of both sexes) have metabasitibial plates. Eardley (1996: 57) stated that the plate is absent in female *S. avius* Eardley, 1996, but this is incorrect. In some the plate is vestigial, replaced by a ring of tubercles delimiting the original margin of the plate (Fig. 86). In others the plate is entire, i.e. a complete, smooth-edged, slightly elevated plate (Fig. 87) that is rounded or slightly pointed apically. A range of intermediate conditions occur. The plate may be largely entire with the margin notched (Fig. 88B), or consist of a posterior carina with tubercles anteriorly (Fig. 88C), or a posterior carina alone (Fig. 88D). A variable number of hairs (five to more than 100) arise from the plate. The hairs are usually simple, but bifid ones are sometimes present. In some species (e.g. *S. albifumus*, *S. calx*, *S. armatipes* (Friese, 1913); Fig. 88A) the plate is densely hirsute such that the plate may be almost completely obscured.

There can be substantial sexual dimorphism in the plate, e.g. *S. bicolor* male has a half-entire metabasitibial plate with only the posterior carina present. In the female the



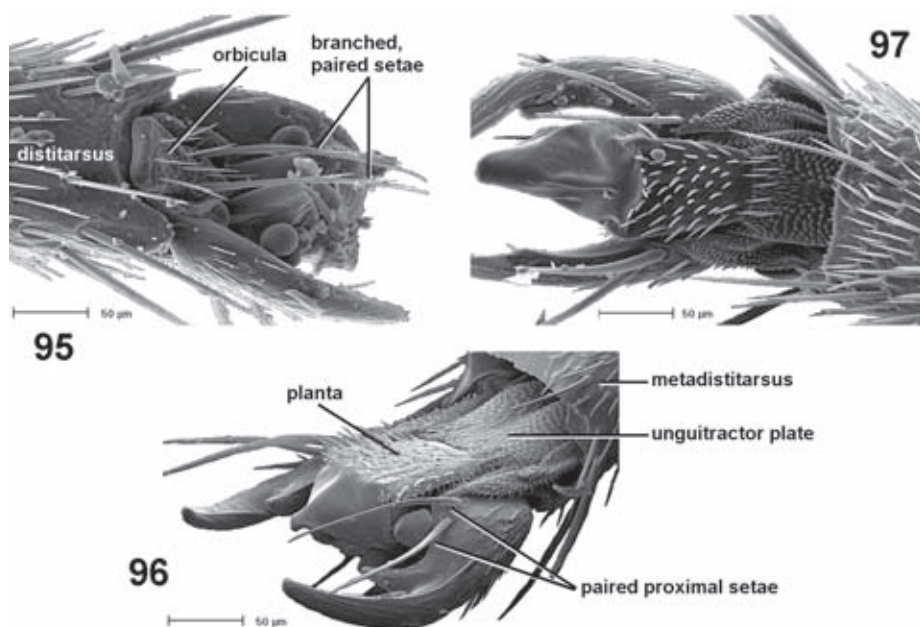
Figs 89–94. Pretarsal structures of *Scapter* females: (89–93) Pretarsal claws and paired, proximal ungual setae: (89) *S. nitidus*, (90) *S. bicolor*, (91) *S. tomentum*, (92) *S. chloris*, (93) *S. cf. erubescens*; (94) Ventral view of pretarsus of *S. armatipes*.

posterior carina is largely reduced to approximately four tubercles with another three anteriorly. In other species (e.g. *S. albifumus*) the plates may be similar in both sexes.

Pretarsal claws and associated structures

The pretarsal claws are either simple (e.g. Fig. 89) or variably toothed (Figs 90–93). When toothed, the pre-apical (sub-apical) tooth is shorter than the outer tooth (the pre-apical tooth varies from 1/2 to 3/4 of the length of the outer tooth). The pre-apical tooth may be rather blunt (Fig. 91) or sharp (Fig. 92); this is possibly wear-related.

Two long, tapering setae arise on the proximo-ventral section of each pretarsal claw, as discussed by Michener (1944: 183) and Eickwort (1969: 350). These setae appear to be found in all bees, although in *Apis* only one seta is present (Erickson *et al.* 1986: 152), and are here termed *paired, proximal ungual setae*. In most *Scapter* species both setae are simple, spirally-grooved hairs (Figs 90–93; near fig. 12 of Braue (1913)). In a



Figs 95–97. (95) Orbicula of female *S. bicolor*, (96, 97) Ventral views of pretarsi of females *S. chloris* and *S. bicolor* respectively.

minority of taxa, the more basal seta is spirally grooved and the outer seta branched (Fig. 89; near fig. 18 of Braue (1913)), or both are branched (Fig. 94).

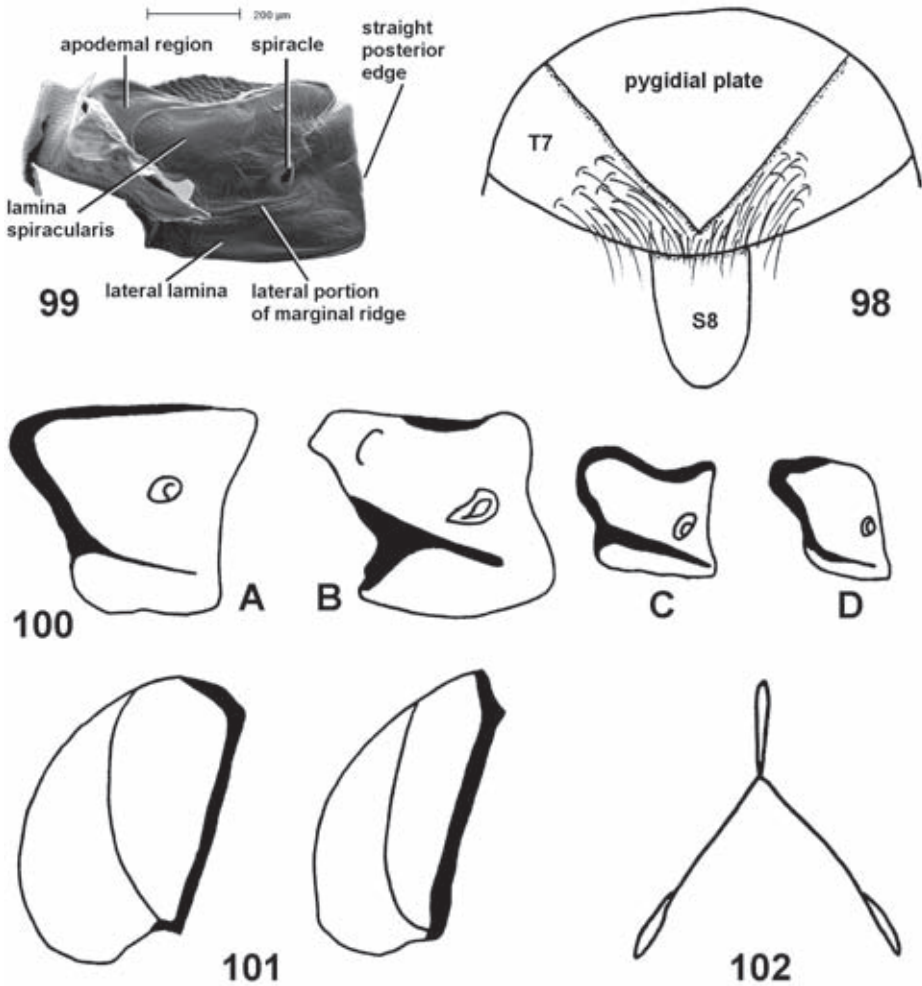
The *orbicula* (manubrium of Snodgrass (1956) and Eickwort (1969)) is a sclerite that occupies the space between the distitarsus and arolium (Fig. 95), and mediates the expansion of the arolium (Federle *et al.* 2001), which is the principal adhesive device of bees. This sclerite tapers apically and is covered in approximately seven to 10 setae. The two apical-most setae are significantly longer than the other setae and usually weakly plumose (e.g. *S. capensis*, *S. chloris*, *S. niger*, *S. bicolor*) or simple (e.g. *S. cf. erubescens* (Friese, 1925) Fig. 93).

The *unguitractor plate* is a sub-quadrate sclerite covered largely in squamous microtrichia (Fig. 96) and is involved in the flexion of the claws and unfolding of the arolium (Gorb 1996; Federle *et al.* 2001). Medially the microtrichia become more tapered and spiculiform. Along the apical edge of the plate are approximately 10 short, simple chaetae. The base of the plate is notched medially. The unguitractor plate is uniform in all *Scrapper* species examined.

The *planta* is a sub-quadrate sclerite lodged between the pretarsal claws and furnished with approximately 40–50 short hairs. In most *Scrapper* species the hairs are simple (Figs 96, 97), but in certain taxa the hairs are distinctly branched (Fig. 94).

Sternum 8

Eardley (1996: 38) and Ascher and Engel (*in* Engel 2005: 13) noted that in *Scrapper* the male S8 is elongate with the apex of the apical process protruding externally, and superficially recalling a pygidial plate. This characteristic is observed in all *Scrapper* species, although the amount of the S8 protruding varies. The S8 is internalised in most



Figs 98–102. (98) Posterior view of T7, pygidial plate and S8 of male *Scapter heterodoxus*; (99–102) Details of sting apparatus of *Scapter* females: (99) Lateral view of T7 of *S. chloris*, (100) T7 of *S. heterodoxus* (A), *S. niger* (B), *S. nitidus* (C), *S. pruinosus* sp. n. (D), (101) T8 of *S. niger* (left) and *S. heterodoxus* (right), (102) Furcula of *S. chloris*.

other colletids, but in the paracolletine *Leioproctus* (Colletinae *sensu* Michener) a similar condition is observed: ‘S8 with apical process ending in rounded, beveled area that is exposed at rest and resembles a pygidial plate’ (Michener 1989: 632). Figure 98 shows the protruding S8 in ♂ *S. heterodoxus*.

Pygidial plate

The pygidial plate is used to tamp or pound soil in the brood chambers (Batra 1964; 1968: 124; Stockhammer 1966: 183; Michener 2000: 32). The pygidial plate is found in all female *Scapter* species. It tapers gradually apically with a rounded apex, is hairless and has smooth edges. The surface of the plate may be granular (Fig. 7). Males of several *Scapter* species also have a pygidial plate (Fig. 98, *contra* Ascher & Engel in

Engel 2005). The pygidial plate is particularly well-developed on the ♂ of *S. heterodoxus* (Fig. 98), less so in other males bearing the plate.

Sting apparatus

The sting apparatus is an intricate structure enclosed by T6 and S6. The final terga (T7 and T8) have become internalised (the corresponding sterna have apparently been lost), and become intimately associated with the sting. Each tergum is divided into two halves, which are unconnected in bees. The sting apparatus is weakly sclerotised in *Scrapper*, and the details are not easily discerned using light microscopy.

Packer (2003) has comprehensively reviewed the sting apparatus across all the major bee clades, and illuminated a range of structural diversity. Packer related some of that structural diversity to phylogeny, but did not discuss the implications for colletid phylogeny in any substantial detail. Toro (1973; cited in Packer 2003) and Aravena and Toro (1985) have investigated parts of the sting (particularly T7 and T8) in the paracolletine *Leioproctus* and xeromelissines. Aside from these studies, and the data provided by Packer (2003), the sting morphology of colletids is largely undescribed.

Terminology for the parts of the sting apparatus has varied from author to author (e.g. Snodgrass 1956; Packer 2003; Rightmyer 2004). The terminology used by Rightmyer (2004) and Grimaldi and Engel (2005) is adopted here.

T7 is largely similar in the *Scrapper* species examined. It is a pair of sub-quadrate, spiracle-bearing, weakly sclerotised sclerites. Features of the sclerite are labelled in Figure 99. The lateral and medial portions of the *marginal ridge* taper shortly before the posterior edge. The *spiracle* is laterally-positioned in the posterior half of the sclerite (Figs 99, 100). The posterior edge is straight (e.g. *S. chloris*) to weakly curved (e.g. *S. niger*, Fig. 100B). The anterior edge is weakly to strongly curved (Figs 100A–D). The *apodemal process* may be weakly to strongly produced (Figs 100A–D). *Scrapper* lacks the *digitiform process* of Euryglossinae, although Packer (2003: 14) reported ‘a similar but flatter structure in *Scrapper*’. Unlike the Euryglossinae, the spiracle is not posteriorly-positioned, i.e. opening onto the posterior edge (Packer 2003, fig. 3c). T7 of *Scrapper* is strongly divergent from those illustrated for *Hylaeus* (Hylaeinae) and *Chilicola* Spinola (Xeromelissinae) (Packer 2003, figs 3d, 3e).

T8 is a pair of largely transparent, kidney-shaped sclerites, each divided into two sections by a *medial carina* (Fig. 101). The *condylar ridge* or condylar ridge area is straight to strongly curved in *Scrapper* (Fig. 101). The *gonangulum* (*first valvifer*) is a small, triangular sclerite that articulates with T8 dorso-posteriorly. In *S. chloris* the *dorsal angle* has two distinct articulation points, but in other scrapperines there appears to be only one point. The *second gonocoxa* (*second valvifer*) is confluent with the *gonoplac* (*gonostylus*) and lies adjacent to the actual sting shaft. The *apodeme of the second gonocoxa* is approximately 0.75–1× breadth of the gonocoxal body. The *furcula* is a thin, Y-shaped sclerite (Fig. 102). In the *Scrapper* species examined there is much variation in the relative lengths of the *dorsal* and *ventral arms*. In *S. chloris* the dorsal arm is 0.5× the length of the ventral arm, but in *S. nitidus* and *S. heterodoxus* the dorsal arm is approximately equal in length to the ventral arm. The ventral arms are widely splayed (large angle between arms). The dorsal arm is strongly laterally compressed. Packer (2003, fig. 11e) illustrated *Colletes*, where the ventral arms are moderately splayed and much longer than the dorsal arm (ventral arms 8× length of dorsal arm).

TAXONOMY

Scrapter pruinosus Davies, sp. n.

Figs 86, 103–109

Etymology: Latin *pruinus* (frosty, covered in hoar-frost or ice). In allusion to the characteristic vestiture of this bee that affords it a frosted appearance (Figs 103, 104, 105).

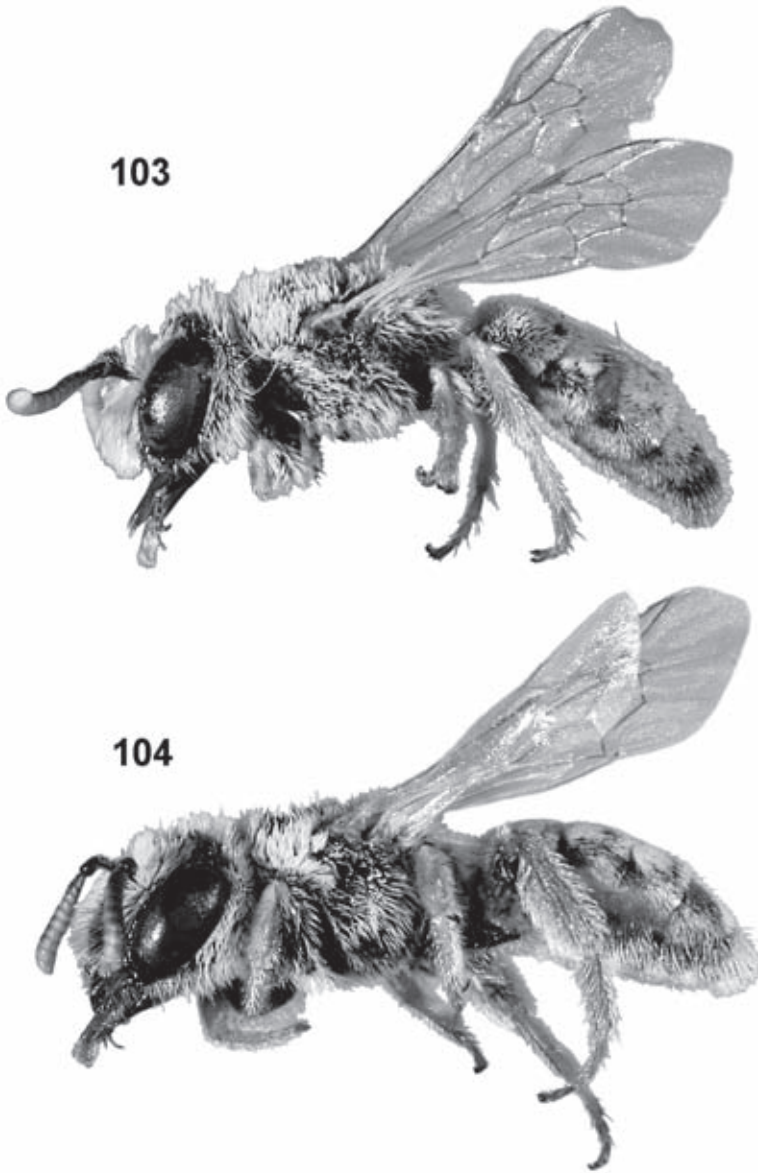
Diagnosis: A tiny bee characterised by its distinctive ‘hoar-frost’ vestiture, yellowish mandibles, bright yellow legs, and partially red T1–3. Further features include fairly dense (♀) to very dense (♂) mesoscutum punctation, lack of a clypeal sulcus, tuberculate metabasitibial plate (♀), deeply cleft claws and narrow facial foveae (bottom of fovea visible). The ♂ *S. pruinosus* keys out to *S. avius* Eardley; it may also exit at *S. caesariatus* Eardley (because of the thick vestiture on the tergal discs), but the reddish metasoma, lack of reticulate sculpture on the mesoscutum, and half-entire (as opposed to entire) metabasitibial plate are diagnostic characters. The ♂ *S. pruinosus* is strikingly similar to *S. avius* but the dense metasomal vestiture is characteristic, the terminalia are distinct (see Eardley 1996, figs 32–34 for *S. avius*) and *S. avius* does not have a reddish metasoma. The ♀ *S. pruinosus* keys to *S. avius* but the thick, white vestiture on the mesoscutum and metasoma of *S. pruinosus* is distinctive. Further T2–4 is all orange in *S. avius* but banded black and orange in *S. pruinosus*, and the prepygidial fimbria in *S. avius* has some black hairs (all white in *S. pruinosus*).

Description:*Male.*

Measurements ($n=4$): total body length 5.9 mm, head length 1.5 mm, head width 1.8 mm, lower interocular distance 1 mm, upper interocular distance 1.3 mm, interantennal distance 0.4 mm, antennocular distance 0.2 mm, length of clypeus 0.6 mm, length of eye 1.2 mm, length of facial fovea 0.4 mm, maximum width of facial fovea 0.04 mm, mesoscutum length 1 mm, mesosoma length 2 mm, forewing length 3.9 mm, length of pterostigma 0.6 mm, maximum width of pterostigma 0.1 mm, length of marginal cell beyond pterostigma 0.8 mm, length of marginal cell 1.1 mm, length of free-part of marginal cell 0.7 mm, metatibia length 1.2 mm, metabasitarsus length 0.7 mm.

Vestiture: With the naked eye, the frosty-white, short vestiture is immediately striking and distinctive. Clypeus, supraclypeal area and lower paraocular areas completely obscured by dense, white, decumbent, minutely plumose (‘bristly’) hairs. Frons, vertex, upper paraocular area with sparse, erect, white hairs (integument easily discernible). Mesoscutum, scutellum and metanotum thickly covered in short, decumbent to sub-erect, short, stout, bristly hairs. Sides of mesosoma with fairly dense, white, bristly vestiture. Tergal discs thickly covered in short, dense, decumbent, bristly, white hairs, most of integument not visible. T6 and T7 hairs longer and more golden. Sternal discs have very sparse, longish hairs (contrasting notably with tergal vestiture).

Integumental colour: Principally black bar metasoma and legs. Protibia and protarsi bright yellow (protibia with pale brownish patch anteriorly). Apical end of profemur orange-yellow. Mid- and hind-leg with similar colour pattern. Antenna brownish above, bright yellow below (on F2–5 dorsal brown patches reduced, most of flagellomere yellow). Mandibles apically black, basal 2/3 yellow. T1, T2 and T3 with posterior band



Figs 103, 104. Lateral views of *Scrapper pruinosus* sp. n. male (103) and female (104).

along marginal zone orange-red, remainder of tergal segment black. T4 and T5 mainly black. All sterna orange-yellow.

Head (Prosoma): Clypeus heavily punctate (interspace $<0.5 \times$ puncture diameter), narrow interspaces smooth and shiny, no medio-longitudinal clypeal sulcus, ventral margin of clypeus slightly emarginate. Supraclypeal area weakly elevated with dense punctation. Frontal line barely evident. Facial fovea sharply-defined, narrow, shiny and smooth. Paraocular area and frons densely punctate. Inner eye orbits diverging dorsally, proportion



Fig. 105. Dorsal view of female *Scapter pruinosus* sp. n.

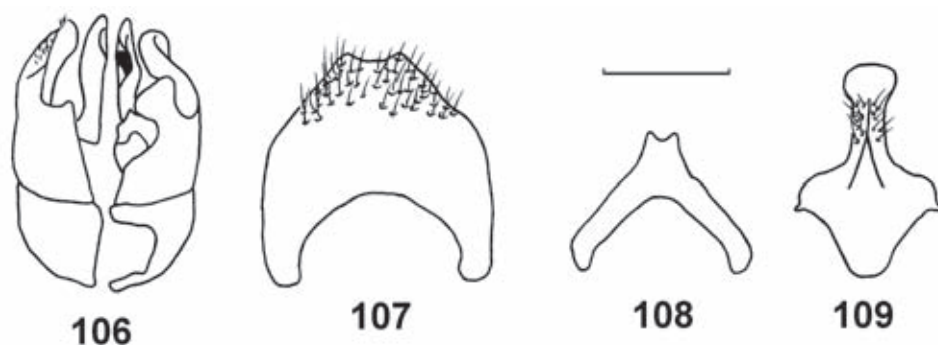
of lower to upper interocular distance 0.8:1. Antenna rather short, just reaching tegula. Labrum longer than broad. Basal area of labrum smooth and elevated with medial protuberance, apical area of labrum hairy.

Mesosoma: Lateral ridge of pronotum not strongly elevated but narrow-edged. Oblique lateral sulcus of pronotum well-developed, terminating dorsad of pronotal ridge. Mesoscutum heavily punctate (interspace $<0.5 \times$ puncture diameter), narrow interspaces smooth and shiny. Median line moderately impressed, notaulus barely evident. Scutellum and metanotum sculpture similar to mesoscutum. Propodeum angulate. Propodeal triangle basal area with sharply-defined, irregular, mostly longitudinal carinae; interspaces roughened. Mesepisternum smooth, shiny and densely punctate (interspace $<0.5-1 \times$ puncture diameter). Pre-episternal groove strongly impressed, pitted throughout.

Legs: Metabasitibial plate only with posterior carina present. Pretarsal claws deeply cleft.

Metasoma: Tergal discs smooth, shiny and densely punctate. T2 fovea ovoid. Pygidial plate absent.

Terminalia: Gonobase large, inner margin of gonocoxite toothed, gonoforceps divided into two surfaces by medial, longitudinal ridge; outer surface concave and moderately hairy, inner surface undistinguished, rather flat with few hairs (Fig. 106). Penis valves long, narrow and slightly exceeding gonoforceps in length (Fig. 106). Ventrally gonoforceps with large ventral process (Fig. 106). Well-defined digitus and cuspis in volsella (Fig. 106). S6 weakly emarginate posteriorly with broad field of hairs (Fig. 107). S7 simple in form, weakly emarginate posteriorly forming two points (Fig. 108). S8 posterior region elongate, posterior plate sub-truncate, posterior process fairly hairy (Fig. 109).



Figs 106–109. *Scrapper pruinusos* sp. n., terminalia: (106) genitalia (dorsal and ventral views), (107–109) S6–8. Scale bar = 0.4 mm.

Female.

Measurements ($n=4$): total body length 6.9 mm, head length 1.7 mm, head width 2.1 mm, lower interocular distance 1.3 mm, upper interocular distance 1.4 mm, interantennal distance 0.4 mm, antennocular distance 0.4 mm, length of clypeus 0.6 mm, length of eye 1.3 mm, length of facial fovea 0.6 mm, maximum width of facial fovea 0.03 mm, mesoscutum length 1.2 mm, mesosoma length 2.3 mm, forewing length 4.5 mm, length of pterostigma 0.7 mm, maximum width of pterostigma 0.2 mm, length of marginal cell beyond pterostigma 1.0 mm, length of marginal cell 1.2 mm, length of free-part of marginal cell 0.7 mm, metatibia length 1.4 mm, metabasitarsus length 0.9 mm.

Vestiture: Generally similar to ♂. Face thick, white, bristly hairs (especially dense on paraocular area and frons). Vertex sparse, erect, white hairs. Gena dense, appressed, bristly, white hairs (integument largely obscured). Mesoscutum, scutellum and metanotum thickly covered in short, erect, bristly hairs (integument not completely obscured, though). Sides of mesosoma similar but longer, sparser hairs. Metasomal terga with very dense, white, short, bristly vestiture largely obscuring integument. S1 and S2 with long, plumose, white hairs forming fairly thick scopa. Remaining sterna with a few plumose hairs, but vestiture weak. Sparse brush on anterior (outer) surface of probasitarsus composed of simple and branched hairs. Metatibial scopa and prepygidial fimbria all white.

Integumental colour: Mainly black, posterior third of T1–5 bright orange. S2–4 orange, S5–6 dark orange-brown. All tibia and tarsi yellow-orange, but metadistitarsus dark orange-brown. Apex of pro- and mesofemur yellow-orange. Undersides of antenna yellow.

Head (Prosoma): Clypeus smooth, shiny, dense punctation (interspace about $0.5\times$ puncture diameter), no medio-longitudinal clypeal sulcus. Supraclypeal area weakly elevated with dense punctation. Paraocular area and frons with dense punctation, smooth interspaces. Facial fovea narrow and smooth. Labrum longer than broad, elevated basal zone with medial protuberance. Glossa apex weakly emarginate. Galeal comb comprising approximately 12 teeth. Maxillary palp slightly exceeding galeal apex in length (last two palpomeres protruding).

Mouthparts: Weakly bilobed glossa with strong glossal brush. Maxillary palp quite long, slightly exceeding galea apex. Labial palp short, falling short of glossa apex.

Mesosoma: Lateral ridge of pronotum rather weakly developed, narrow-edged. Oblique lateral sulcus of pronotum well-developed, terminating dorsad of pronotal ridge. Mesoscutum fairly dense to dense punctation (interspace about 0.5–1× puncture diameter). Scutellum and metanotum similar mesoscutum. Mes- and metepisterna fairly dense to dense punctation, smooth interspaces. Propodeum angulate. Propodeal triangle basal area with longitudinal carinae and roughened interspaces.

Legs: Metabasitibial plate reduced to very short, posterior carina basally and about 6 small tubercles delineating outline of plate (Fig. 86). Pretarsal claws deeply cleft, pre-apical tooth slightly shorter than outer tooth.

Metasoma: Tergal discs smooth, shiny and heavily punctate. T2 fovea ovoid. Pygidial plate smooth, parallel-sided, rounded apically.

Terminalia: T7 with strongly produced apodemal region, posterior edge almost straight, spiracle placed far back but not opening onto posterior edge, lateral lamina narrow (approximately 0.1× breadth of lamina spiracularis). Dorsal arm of furcula approximately 0.5× length of ventral arm. Apodemal ridge of 2nd gonocoxa straight. Gonoploc parallel-sided, hairy apically.

Holotype: ♂ NAMIBIA: Lüderitz (26°35'S:15°07'E), 7.xii.1994, M. Kuhlmann (SANC).

Paratypes: 11♂ and 10♀ with same label data as holotype (all MKPC, except 1♀ in SANC).

Distribution: *S. pruinus* is only known from the type locality of Lüderitz, which is a town at sea-level in southern Namibia. The Lüderitz area is a harsh, hyper-arid environment with cold buffeting Atlantic winds and a sparse, dwarf shrubland vegetation. Lüderitz falls near the northern edge of Succulent Karoo biome (and winter rainfall zone).

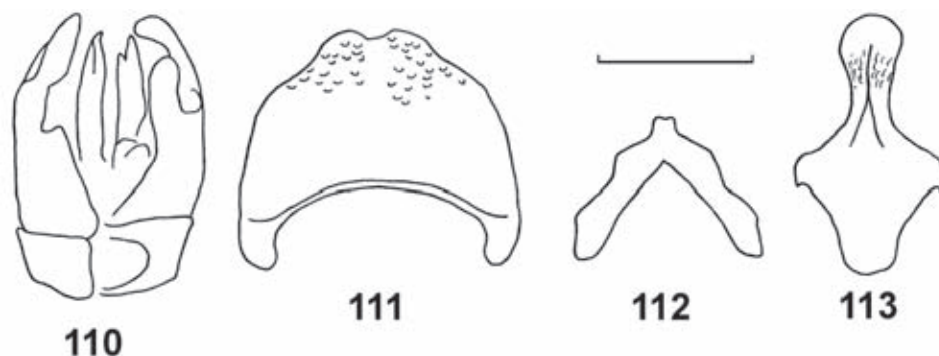
Biology: There are no relevant floral records.

***Scrapter pyretus* Davies, sp. n.**

Figs 110–114

Etymology: Greek *pyretos* (burning hot, fiery). In allusion to the sweltering type locality in Namibia, and the fiery orange metasoma in both sexes.

Diagnosis: *S. pyretus* is a tiny black bee with an orange-red metasoma (Fig. 114). Other noteworthy features are the deep, slit-like facial foveae, largely yellow mandibles, slight yellow tinge to pronotal lobe, tuberculate metabasitibial plate in the ♀, and simple claws in the ♀. The ♂ keys to *S. luridus* because of the orange-yellow scape. *S. pyretus* ♂, though, is easily distinguished from *S. luridus* ♂ by (a) the orangish metasoma (black in *S. luridus*), (b) its smaller body length (approximately 8–9 mm in *S. luridus*), (c) the different facial foveae (shallow and indistinct in *S. luridus*), (d) the near-absent lateral pronotal ridge (sharp and well-defined in *S. luridus*) and (e) the strongly divergent terminalia (see Eardley 1996, figs 78–80 for *S. luridus*). In general facies, the ♂ *S. pyretus* recalls *S. avius* or *S. calx*, but the mostly orange metasoma and orangish scape are distinctive. The ♀ keys out at *S. avius*, and is superficially similar to that species. The ♀ *S. pyretus* can be distinguished by (a) its largely yellow mandibles (dark red-brown to black in *S. avius*), (b) blunt lateral pronotal ridge (sharp-edged and well-



Figs 110–113. *Scrapper pyretus* sp. n., terminalia: (110) genitalia (dorsal and ventral views), (111–113) S6–8. Scale bar = 0.4 mm.

defined in *S. avius*), and (c) slit-like facial fovea with the bottom of the fovea not visible (*S. avius* facial foveae are also narrow but the bottom is clearly visible with reticulate sculpture).

Description:

Male.

Measurements ($n=4$): total body length 5.8 mm, head length 1.2 mm, head width 1.5 mm, lower interocular distance 0.8 mm, upper interocular distance 1.0 mm, inter-antennal distance 0.3 mm, antennocular distance 0.2 mm, length of clypeus 0.4 mm, length of eye 0.9 mm, length of facial fovea 0.3 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 0.8 mm, mesosoma length 1.8 mm, forewing length 3.7 mm, pterostigma length 0.5 mm, maximum width of pterostigma 0.2 mm, marginal cell length 0.9 mm, length of marginal cell beyond pterostigma 0.7 mm, length of free part of marginal cell 0.6 mm, metatibia length 1.1 mm, metabasitarsus length 0.7 mm.

Vestiture: Clypeus, supraclypeal area, and lower paraocular area thickly covered in decumbent, white, bristly hairs (integument obscured). Vertex with sparse, erect, longish, white hairs. Gena densely covered in shortish, white hairs. Mesoscutum fairly densely covered in short, whitish, erect hairs (integument visible). Scutellum and metanotum similar to mesoscutum. Mesepisternum hairless dorsally, but thickly hairy below. Metepisternum largely nude. T2–4 with bands of very short, bristly, white hairs along graduli. Sterna very weakly hairy with feeble posterior hairbands S3–5.

Integumental colour: Mostly black except for metasoma and legs. Scape, pedicel and flagellomeres orange-yellow, dorsal surface of flagellomeres dark brown. Mandible largely yellow except for apical black tip. Pronotal lobe dark brown with slight yellow tinge. Protibia and protarsi yellow. Profemur and protrochanter brown with orange tinge. Mid- and hindlegs similar colour pattern to foreleg. T1 black, slightly orange posteriorly. T2 orange (fovea and area immediately adjacent black). T3 orange-brown. T4–6 black. T7 orange.

Head (Prosoma): Clypeus densely punctate (interspace $<0.5 \times$ puncture diameter), smooth and shiny interspaces, no medio-longitudinal clypeal sulcus, lower edge of clypeus emarginate. Supraclypeal area protuberant, anterior face of supraclypeal area densely

punctate (interspace $<0.5\times$ puncture diameter). Paraocular area and frons densely punctate. Frontal line apically carinate. Facial fovea very narrow, slit-like. Vertex densely punctate, not carinate. Gena densely punctate. Inner eye orbits diverging slightly dorsally, proportion of lower to upper interocular distance 0.8:1. Antenna rather short, just reaching tegula.

Mesosoma: Pronotal lateral ridge weak. Mesoscutum densely punctate (interspace $0.5\text{--}1\times$ puncture diameter), interspaces smooth and shiny, median line weakly impressed. Scutellum and metanotum similar sculpture to mesoscutum. Propodeum strongly angulate. Propodeal triangle with irregular network of carinae on basal area. Basal area of propodeal triangle quite long, $2\times$ length of metanotum. Mesepisternum fairly dense punctation, slightly roughened between punctures. Upper half of metepisternum with three transverse carinae in some specimens.

Legs: Metabasitibial plate with only posterior carina present, small apical tubercle sometimes present. Pretarsal claws deeply cleft.

Metasoma: Tergal discs with dense punctation and smooth interspaces. T2 fovea elongate ovoid. Pygidial plate absent.

Terminalia: Gonobase large, inner margin of gonocoxite toothed posteriorly, gonoforceps curved inwards posteriorly, lightly hairy (Fig. 110). S6 weakly emarginate posteriorly, weak ridge adjacent to apodemes (Fig. 111). S7 posteriorly tapering to weakly emarginate point, outer margin of anterior arms with small protuberance (Fig. 112). S8 apical process short, fairly hairy, rounded (Fig. 113).

Female.

Measurements ($n=4$): total body length 6.3 mm, head length 1.3 mm, head width 1.7 mm, lower interocular distance 1.0 mm, upper interocular distance 1.1 mm, inter-antennal distance 0.3 mm, antennocular distance 0.3 mm, length of clypeus 0.5 mm, length of eye 1.0 mm, facial fovea length 0.5 mm, maximum width of facial fovea 0.02 mm, mesoscutum length 0.9 mm, mesosoma length 2.0 mm, forewing length 3.9 mm, pterostigma length 0.5 mm, maximum width of pterostigma 0.2 mm, marginal cell length 1.0 mm, length of marginal cell beyond pterostigma 0.8 mm, length of free part of marginal cell 0.7 mm, metatibia length 1.2 mm, metabasitarsus length 0.7 mm.

Vestiture: Face largely naked, sparse white hairs surrounding antennal sockets and feeble fringe to ventral margin of clypeus. Sparse, scattered, short white hairs on mesoscutum, thicker on scutellum and metanotum. Sides of mesosoma weakly hairy. T2–4 with bands of short, white hairs along graduli, expanding out onto disc on T4. Prepygidial fimbria thick, white, bristly hairs. Metatibial scopa all white hairs. S2 plumose, white hairs, remainder of sterna with sparse, white hairs. Brush on anterior (outer) surface of probasitarsus with simple hairs.

Integumental colour: Mainly black. Scape and pedicel brownish with slight orange tinge. Flagellomeres ventrally yellow, dorsally dark brown. Mandibles mostly yellow-orange. T1–4 all orange. T5 mainly black. T6 orangish. Trochanter and femur on all legs brown with orange tinge. All tibia and tarsi orange-yellow.

Head (Prosoma): Clypeus with fairly dense punctation (interspace $1\text{--}1.5\times$ puncture diameter), interspaces shiny and superficially smooth (but very faintly reticulate), no medio-longitudinal clypeal sulcus, lower edge of clypeus medially emarginate. Supra-



Fig. 114. Lateral view of female *Scapter pyretus* sp. n.

clypeal area strongly protuberant above adjacent antennal sockets. Anterior face of supraclypeal areas with rather sparse punctation, shiny with faint reticulation. Paraocular area, frons and vertex densely punctate (interspace $0.5\text{--}1\times$ puncture diameter), interspaces smooth and shiny, vertex not carinate. Frontal line apically carinate. Facial fovea slit-like. Eyes diverge very slightly dorsally, proportion of upper to lower interocular distance $1.0:1.1$. Antenna just reaches tegula.

Mesosoma: Lateral ridge of pronotum weak. Mesoscutum densely punctate (interspace $0.5\text{--}1\times$ puncture diameter), anterior interspaces with faint reticulation, remainder smooth. Median line moderately impressed, notaulus very weak and barely evident. Scutellum sparsely punctate, interspaces shiny, superficially smooth with very faint reticulations. Propodeum strongly angulate. Basal area of propodeal triangle with short, longitudinal carinae, remainder of triangle roughened. Basal area of propodeal triangle approximately $1.7\times$ longer than metanotum. Mesepisternum densely punctate with reticulate interspaces, pre-episternal groove pitted throughout.

Legs: Metabasitibial plate reduced to a ring of seven to nine irregularly-shaped tubercles. Pretarsal claws simple.

Metasoma: Tergal discs with dense punctation and smooth interspaces. T2 fovea ovoid. Pygidial plate weakly tapering, rounded, dorsal surface smooth.

Terminalia: T7 sub-quadrate with moderately produced apodemal region, posterior edge curved and slightly produced ventro-posteriorly, spiracle placed far back but not opening onto posterior edge, lateral lamina fairly narrow (approximately $0.2\times$ breadth of lamina spiracularis). Dorsal arm of furcula sub-equal in length to ventral arms. Condylar ridge area of T8 strongly curved. Apodeme of T8 extends beyond tergum.

Holotype: ♂ NAMIBIA: Gaub Pass ($23^{\circ}30'S:15^{\circ}46'E$), 19.iii.1997, F.W. & S.K. Gess (AMGS).

Paratypes: 6♂ and 4♀ with same label data as holotype (AMGS) and 7♂ and 8♀ from Namibia, Swakop River ($22^{\circ}41'S:14^{\circ}35'E$), on road to Goanikontes, 11.iv.1998, F.W. & S.K. Gess (AMGS).

Distribution: Namibian endemic, only known from the Gaub Pass and Swakop River area.

Biology: Specimens (both sexes) were caught visiting the yellow flowers of *Tetraena* (= *Zygophyllum*) *simplex* (L.) Beier & Thulin (Zygophyllaceae) in dry river-beds. The bees have been captured in March–April, suggestive of a late summer bee.

Scrapter viciniger Davies, sp. n.

Figs 115–118

Etymology: Latin *vicinus* (neighbouring, near, close to); Latin *niger* (black). In allusion to its superficially similar appearance to *S. niger*.

Diagnosis: *S. viciniger* is very similar in appearance to *S. niger*, and exits at this species in the key in Davies *et al.* (2005). To distinguish this species from *S. niger* the terminalia need to be extracted. The toothed inner margin of the gonocoxite of *S. viciniger* is characteristic. Other noteworthy features of *S. viciniger* include a carinulate vertex and frons, largely smooth mesoscutum, entire metabasitibial plate, propodeal triangle with uniform sculpture, and dark (as opposed to yellowish) tarsi.

Description:**Male.**

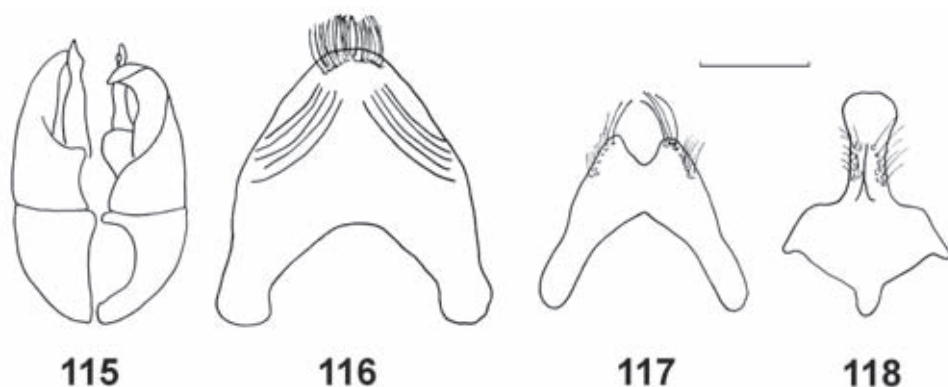
Measurements ($n=4$): total body length 8.9 mm, head length 1.8 mm, head width 2.2 mm, lower interocular distance 1.3 mm, upper interocular distance 1.6 mm, inter-antennal distance 0.4 mm, antennocular distance 0.4 mm, length of clypeus 0.6 mm, length of eye 1.3 mm, length of facial fovea 0.5 mm, maximum width of facial fovea 0.1 mm, mesoscutum length 1.2 mm, mesosoma length 2.6 mm, forewing length 6.1 mm, pterostigma length 0.9 mm, maximum width of pterostigma 0.2 mm, marginal cell length 1.5 mm, length of marginal cell beyond pterostigma 4.8 mm, length of free-part of marginal cell 1.0 mm, metatibia length 1.7 mm, metabasitarsus length 1.1 mm.

Vestiture: Clypeus and lower paraocular area with thick, appressed, minutely plumose, white hairs (underlying integument completely obscured). Supraclypeal area, upper paraocular area frons and vertex sparse, erect, plumose greyish hairs. Gena fairly thick, white, plumose hairs. Mesoscutum with moderate cover of long, erect, weakly plumose, greyish hairs (underlying integument easily visible). Scutellum and metanotum similar to mesoscutum but hairs thicker and base of hairs dark, imparting brownish impression to vestiture. Plumose, greyish hairs, hairs thicker on propodeum with dark bases creating brownish impression. T1 sparse hairs anteriorly. T2–4 fairly dense, sub-erect, minutely plumose whitish hairs, thicker anteriorly (underlying integument can easily be seen). No tergal bands. S2–5 incurved, sparse, minutely plumose hairs, no distinct bands on sterna.

Integumental colour: Mainly black. Slight orange tinge to ventral surface of antenna. Metasoma with orange-brown tinge. No yellow on legs or antenna.

Head (Prosoma): Clypeus densely punctate (interspaces $0.5\times$ puncture diameter), interspaces smooth, no medio-longitudinal clypeal sulcus. Supraclypeal area weakly elevated, anterior face of supraclypeal area largely punctureless, smooth and shiny. Lower paraocular area densely punctate (interspaces $0.5\times$ puncture diameter). Frons, upper paraocular area and vertex strongly carinulate. Facial fovea narrow, shallow ovoid with roughened sculpture inside. Gena with fairly dense punctation, near-carinulate. Antenna long, when extended backwards reaches propodeum.

Mesosoma: Pronotum lacking lateral ridge. Mesoscutum densely punctate (interspaces $0.5\times$ puncture diameter), anterior third, lateral edges and posterior edge of mesoscutum roughened, remainder smooth. Scutellum and metanotum similar to mesoscutum but



Figs 115–118. *Scapter viciniger* sp. n., terminalia: (115) genitalia (dorsal and ventral views), (116–118) S6–8. Scale bar = 0.4 mm.

roughened throughout. Pre-episternum and mesepisternum with moderate punctation, coarsely roughened and carinulate. Hypoepimeral area uniformly roughened with no carinae. Metepisternum and sides of propodeum with sparse punctation and uniform coriaceous sculpture (not carinulate). Propodeum near-declivitous. Propodeal triangle with weak, short carinae on narrow basal area, remainder of triangle uniformly coriaceous roughening. Basal area of propodeal triangle approximately same length as metanotum.

Legs: Metabasitibial plate entire. Pretarsal claws deeply cleft.

Metasoma: T1 anteriorly minutely roughened and densely punctate, posterior third shiny and smooth. T2–4 very fine sculpture and densely punctate. T7 with weak pygidial plate. T2 fovea short, weakly-defined ovoid.

Terminalia: Gonobase large, inner margin of gonocoxite conspicuously toothed, gonoforceps curved inwards posteriorly, penis valves narrow (Fig. 115). S6 rounded posteriorly with hair tuft on apex, meso-laterally are two separate sets of curved carinae (Fig. 116). S7 concave posteriorly with tufts of setae postero-laterally (Fig. 117). S8 posterior process rounded and hairy (Fig. 118).

Female. Unknown.

Holotype: ♂ SOUTH AFRICA: *Northern Cape*: Nieuwoudtville Flower Reserve (31°21'56"S:19°08'52"E), 735m, 3.ix.2003, M. Kuhlmann (SANC).

Paratypes: 2♂ with same label data as holotype (MKPC); 6♂ Nieuwoudtville district, Farm Glen Lyon (31°23'50"S:19°08'26"E), 11–12.ix.2003 (MKPC).

Distribution: Only known from the Nieuwoudtville district (Succulent Karoo biome).

Biology: Specimens have been caught on *Oxalis* sp. (Oxalidaceae) and *Eriocephalus ericoides* (L.f.) Druce (Asteraceae). The limited data suggests the flight period is during the austral spring (September).

Scapter niger Lepeletier de Saint-Fargeau & Audinet-Serville, 1828

Scapter niger Lepeletier de Saint-Fargeau & Audinet-Serville, 1828: 403. Type locality: 'Cafrarie'.

Scapter subincertus Cockerell, 1944a: 405. Type locality: Rapenburg, Cape Flats, Cape Town, Western Cape. **Syn. n.**

Scapter brunneipennis Cockerell, 1944a: 406. Type locality: Mossel Bay, Western Cape. **Syn. n.**

S. subincertus (Fig. 119) was briefly described from females collected at Rapenburg, Western Cape, in early October by Rowland Turner. Cockerell (1944a) wondered 'whether this could be the female of *S. niger*, but what I have identified as probably *S. niger*, from Natal, is certainly different'. Cockerell's remarks are rejected because *S. niger* does not occur in KwaZulu-Natal (Eardley 1996: fig. 62), and a *S. subincertus* syntype loaned to GBPD agrees excellently with material from Dassiefontein, Kamieskroon district, Northern Cape, identified as *S. niger* by C.D. Eardley. Identifying features include the presence of a clypeal tubercle, nascent clypeal sulcus, sharply-defined ovoid facial foveae with finely reticulate sculpture, weakly carinulate vertex and frons, dense mesoscutum punctation (interspace 0.5–1× puncture diameter) with smooth interspaces and scattered micropunctures, weakly angulate propodeum (propodeal triangle basal area subequal in length to metanotum) with feeble carinae on propodeal triangle basal area, tuberculate metabasitibial plate, simple claws and brush on anterior (outer) surface of probasitarsus with both simple and branched hairs.

The status of the material identified as probable *S. niger* from KwaZulu-Natal by Cockerell is uncertain; it is possibly in the Natural History Museum, London. Cockerell (1935: 239) also mentioned male bees from KwaZulu-Natal Drakensberg that he tentatively identified as male *S. niger*.

Cockerell (1944a) described *S. brunneipennis* (Fig. 120) from male specimens obtained at Mossel Bay, Western Cape, by Rowland Turner in August 1932. GBPD has examined a syntype, and the genitalia agree closely with that of *S. niger* illustrated by Eardley (1996, fig. 57). Other features include: carinulate frons and vertex, no medio-longitudinal clypeal sulcus, finely reticulate mesoscutum surface with heavy punctation, metabasitibial plate not entire (jagged posterior carina and weak anterior carina), pygidial plate present, and all tarsi and protibia yellowish. The male holotype of *S. niger* in the Paris Museum is apparently now untraceable (C. Villemant *in litt.*).

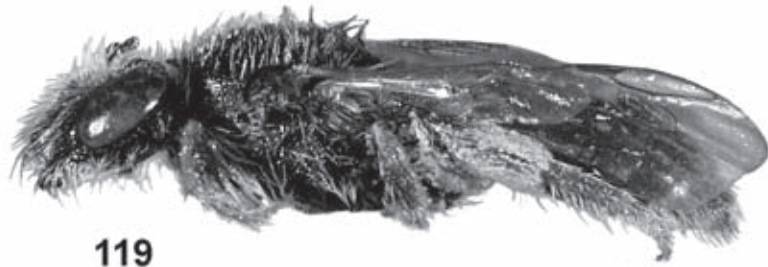
Scrapter leonis Cockerell, 1934

Scrapter leonis Cockerell, 1934: 452. Type locality: Lion's Head, Cape Town, Western Cape.

Scrapter merescens Cockerell, 1944a: 405. Type locality: Worcester, Western Cape. **Syn. n.**

S. merescens (Fig. 121) was perfunctorily described on the basis of seven females from Worcester in the Western Cape collected by Rowland Turner during August to September 1928 (Cockerell 1944a). GBPD has examined a female syntype and found that it is attributable to *S. leonis*. Cockerell (1944a: 406) compared *S. merescens* to *S. leonis*, but distinguished it on the basis of 'duskier wings and the absence of red hair on the scutellum, as well as the broader head'. These seem trifling differences and *S. merescens* is here synonymised with *S. leonis*.

Cockerell (1944a: 406) also mentioned a male specimen from Worcester that he thought may belong to *S. merescens*. GBPD has examined this specimen. The handwritten label by Cockerell reads '*Scrapter merescens*, probable M, C[oc]k[er]ell'. Cockerell did not describe this male in his 1944 paper, and clearly did not intend it to form any part of the syntype material. GBPD's examination of the specimen shows that it is unequivocally a specimen of *S. capensis* (Fries) as shown by the lack of a medio-longitudinal clypeal sulcus, carinulate frons and vertex, narrow, shallow facial fovea, leathery mesoscutal sculpture, almost entire metabasitibial plate (slight gap apically), short, plumose tomentum on S2 and S3 and truncate S8 and distinctly bifid claws. As



Figs 119–121. General appearance of *Scrapper* bees: (119) Lateral view of female *S. subincertus*, (120) Dorsal view of male *S. brunneipennis*, (121) Lateral view of male *S. merescens*.



Fig. 122. Dorsal view of male *Scrapter sinophilus* Cockerell.

the male specimen does not form part of the original syntype series, it has no nomenclatural standing and has merely been labelled as a *S. capensis* specimen.

Scrapter algoensis (Friese, 1925)

Polyglossa (*Strandiella*) *algoensis* Friese, 1925: 519. Type locality: Algoa Bay, Western Cape.

Polyglossa (*Polyglossa*) *rufofasciata* Friese, 1925: 518. Type locality: Port Nolloth, Northern Cape.

Scrapter algoensis (Friese): Eardley 1996: 72.

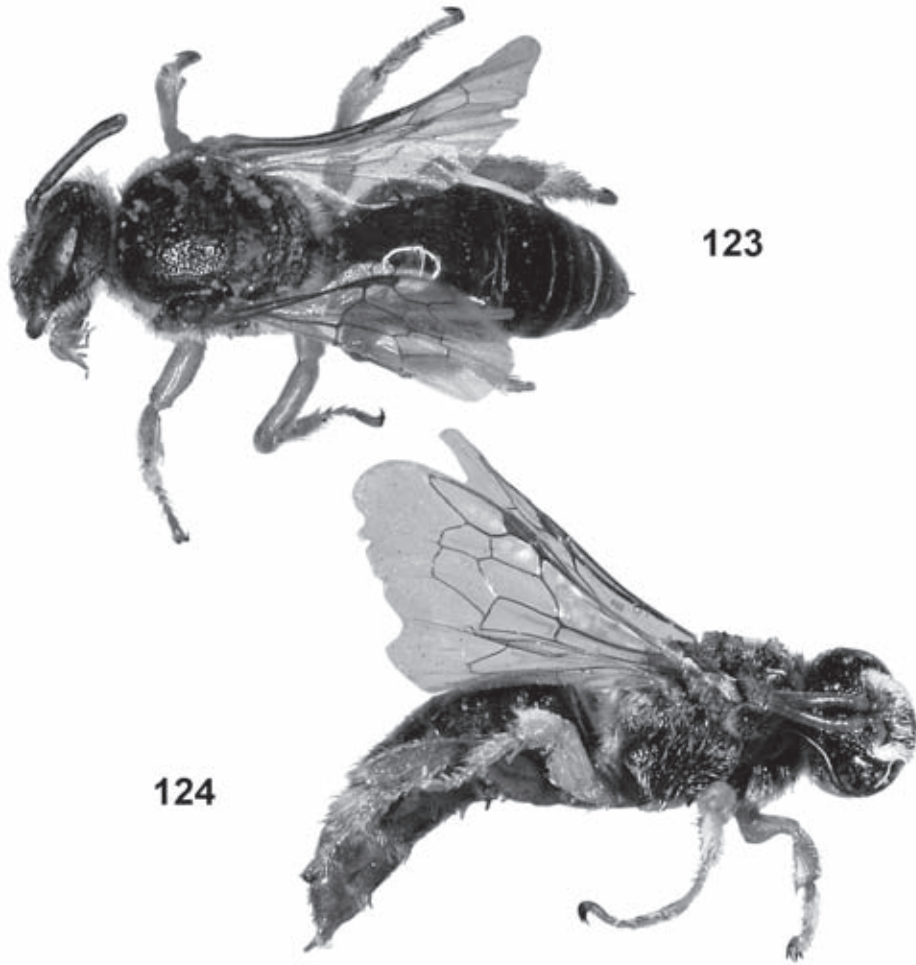
Scrapter sinophilus Cockerell 1944a: 406. Type locality: Mossel Bay, Western Cape. **Syn. n.**

Cockerell (1944a) described *S. sinophilus* (Fig. 122) from 12 males and four females collected by Rowland Turner at Mossel Bay. GBPD has examined four male syntypes which agree well with material identified as *S. algoensis* by C.D. Eardley, in particular the genitalia accord closely (Eardley 1996, figs 67–69). Other relevant features of the males include: no medio-longitudinal clypeal sulcus, antennae long reaching propodeum if extended backwards, vertex and frons not carinulate, mesoscutum with dense punctation and finely reticulate interspaces, propodeum slightly angulate, propodeal triangle with uniform, leathery sculpture throughout, and metabasitibial plate not entire (posterior carina plus a few small tubercles delimiting margin of plate).

Ctenoplectrina ugandica (Cockerell, 1944), **comb. n.**

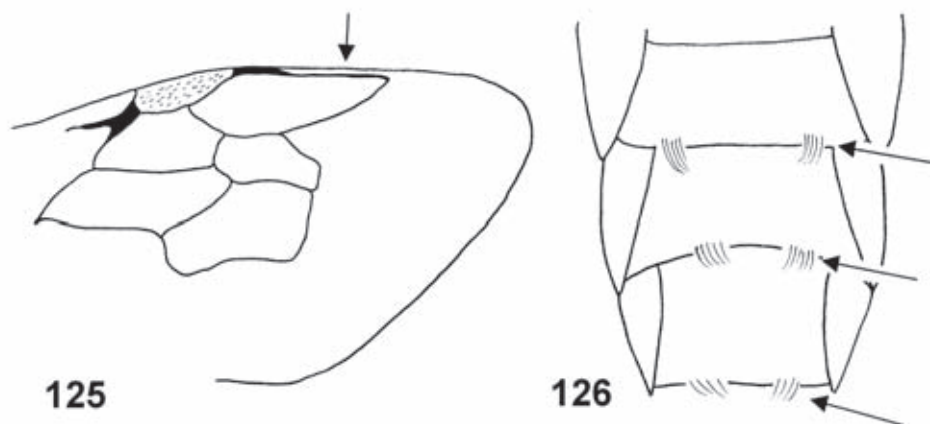
Scrapter ugandica Cockerell 1944b: 805. Type locality: Madi, Uganda.

Cockerell (1944b) described *S. ugandica* on the basis of a single female (Figs 123, 124) collected in May 1927, and he expressed surprise to ‘find this South African genus so far north as Uganda’. Examination of the holotype female indicates that *S. ugandica* is not a colletid, let alone a *Scrapter* species.



Figs 123, 124. Dorsal and lateral views of female *Ctenoplectrina ugandica*.

Dissection of the mouthparts revealed it to have a fairly long, acute glossa. Other features arguing against it being a colletid include the lack of a pre-episternal groove (ignoring *Diphaglossini* and *Hesperocolletes* Michener), lack of arolia and absence of facial foveae. The labial palp segments are sub-equal in length, which suggested some sort of 'short-tongued' bee (possibly in *Andrenidae*, *Halictidae* or *Melittidae*). The general facies of the bee, however, was not similar to these 'short-tongued' taxa, and a stipital concavity with a weak comb was detected during the dissection of the mouthparts. There was also no trace of a galeal comb. These are features of a 'long-tongued' bee. Keying the specimen brought it out at *Ctenoplectrini* (*Apidae*), and this identification was confirmed by the marginal cell being sharply bent away from the costal margin (Fig. 125), a feature Michener and Greenberg (1980: 191) identify as 'a unique synapomorphy of the *Ctenoplectridae*'. Further confirmation was provided by the oil-collecting hairs on S3–5 (Fig. 126). Other characters of this bee include the short, compressed F1–3 (contrasting with other flagellomeres), short, blunt mandibles with



Figs 125, 126. *Ctenoplectrina ugandica*: (125) Apical portion of forewing, marginal cell bent away from costal margin (arrowed), (126) Oil-collecting hairs on S2–4.

weak sculpture, lack of a ventral premental fovea, two submarginal cells, declivitous propodeum, lack of T2 fovea, weak, thin pygidial plate and deeply cleft claws.

There are only two ctenoplectrinid genera, *Ctenoplectra* Kirby and the parasitic *Ctenoplectrina* Cockerell. *S. ugandica* is ascribed to the latter because it lacks a metabasitibial plate and has reduced oil-collecting tufts on the sterna. Michener (2000: 678) admitted one species in *Ctenoplectrina*, but noted 'the diversity among three specimens suggests two species'. Consequently we have moved the species to *Ctenoplectrina*, but left in abeyance its relationship to the only other formally described species, *C. politula* Cockerell.

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